Moose and deer resource selection and co-occurrence in northeast Minnesota

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Dedication

To my parents. My earliest memories are of being out in the woods with you. And for that, I thank you from the bottom of my heart. I also thank you for being so passionate about wildlife and nature that my first word was ‘grouse’. You have always encouraged me to pursue my passions and are unwaveringly supportive in all my pursuits. I love you.

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A note on moose, deer, and *Parelaphostrongylus tenuis*

Preface

A parasite, *Parelaphostrongylus tenuis,* carried by white-tailed deer (*Odocoileus virginianus*) has often been cited as a significant factor contributing to moose (*Alces alces*) population declines. Moose suffer from neurologic disease and usually die when infected with *P. tenuis*. The strength of the three-way relationship between moose, deer, and *P. tenuis,* and the resulting negative impact on moose health, is thought to be driven by deer densities. Despite its importance for moose and deer management, only one peer-reviewed study to date has tested the relationship between deer and moose densities, and therefore the potential for parasite-mediated competition between moose and deer, using empirical data. A deer density threshold above which moose populations declined was identified using the empirical data collected for the study. However, the nature of the data and apparent outliers suggest that the modeling approach used to develop that threshold may not have been appropriate. Here we tested, using data from the original study, whether alternative models, including linear models and negative binomial models would be less sensitive to outliers and could better explain the relationship between deer and moose densities in this study system. We found no evidence in our analysis that moose density decreases as deer density increases. We conclude that while the proposed moose-deer-*P. tenuis* relationship could be partially density dependent, additional factors such as frequency dependence of disease transmission and shared use of resources by moose and deer should also be considered.

Key Words: *Alces alces*, moose, *Odocoileus virginianus*, *Parelaphostrongylus tenuis*, threshold density, white-tailed deer,

Introduction

Parasite-mediated competition happens when a parasite differentially impacts multiple host species that share significant resources on overlapping ranges (Price et al. 1988). Theoretically, an unstable equilibrium and eventual extirpation of the more negatively affected host species will occur when a wide distribution and high prevalence of a parasite is maintained by the less affected host (Schmitz and Nudds 1994). A warming climate that supports range expansions of less affected host species into native ranges of more susceptible species (Harvell et al. 2002, Dawe and Boutin 2016) could increase parasite-mediated competition through the introduction of novel parasites or increased parasite prevalence (Harvell et al. 2002). Therefore, at the margin of a species range, population fluctuations of the most heavily affected host could be severe.

However, parasite-mediated competition at range margins is difficult to detect or document and is poorly understood due to additional factors such as climate change and anthropogenic disturbances that also contribute to host-parasite interactions (Harvell et al. 2002). A classic example is the potential effect of white-tailed deer (*Odocoileus virginianus*) parasites on other ungulates such as moose (*Alces alces*) and woodland caribou (*Rangifer tarandus caribou*). Deer expanded northward into the southern edge of historic moose range in the 1800's and early 1900's, likely because of European settlement and habitat alterations such as widespread logging (Anderson 1972). Consequently, moose were exposed to a novel set of parasites carried by deer. An example of one such parasite that differentially impacts deer and moose is the meningeal worm, *Parelaphostrongylus tenuis* (Anderson 1972). Deer are the definitive host of *P. tenuis* and typically have infection rates of >50% where deer, moose, and gastropod

intermediate hosts are sympatric (Table 1.1). *P. tenuis* infection does not appear to have any negative health impacts on deer. As an incidental host for *P. tenuis*, infected moose present with several neurological symptoms such as lack of fear, remaining in one area for extended periods of time, circling, partial paralysis, tilted head, and nystagmus (Lankester et al. 2007).

P. tenuis cannot exist without the intermediate gastropod hosts and is most common in regions with high deer densities and where forest cover is between >25% and <75% (Wasel et al. 2003). *P. tenuis* prevalence also is negatively correlated with spring and fall temperatures (Wasel et al. 2003). As such, *P. tenuis* infection in deer is low and infection in moose is rare in western North America where deer densities are lower, more open grassland habitats are available, and weather conditions are typically hotter and dryer than those found in moose ranges in the Great Lakes region and in the northeastern U.S. (Wasel et al. 2003).

In North America, there are typically fewer than 0.5 moose / km^2 across the southern edge of moose range where moose coexist with deer (Lankester 2010, DelGiudice 2017). Deer populations in these latitudes fluctuate primarily because of severe winter conditions (Potvin et al. 1981, DelGiudice et al. 2002, Patterson and Power 2002). In these regions of range overlap, *P. tenuis* infection rates in deer are relatively high, ranging from 35-85%, with infection rates generally decreasing along a westward longitudinal gradient (Table 1.1).

There are several examples of moose populations declining during a series of years when deer populations were increasing (Lankester 2010). In northwestern Ontario, for example, when deer populations increased during the 1940's moose populations

declined to the extent that the moose hunting season was closed (Lankester 2010). During the 1990s, the moose population in western North Dakota declined after deer populations expanded northward and increased rapidly (Lankester 2010). Also, during the 1990s and early 2000s, the moose population in northwest Minnesota declined from about 4,000 to fewer than 100 in 2006 (Murray et al. 2006). A historic peak deer density was reached in northeast Minnesota in 2003, followed by a period of about a decade when deer densities were stable or slightly declining (Minnesota Moose Research and Management Plan 2011). During this period the northeast Minnesota moose population declined from an estimated 8,000 individuals in 2006 to about 4,000 in 2014 (DelGiudice 2017).

Moose populations also sometimes increase after deer populations decline (Lankester 2010). In Nova Scotia, a series of three severe winters in the 1950's depressed deer numbers while moose numbers increased (Pulsifer and Nette 1995). A similar increase in the moose population also happened during a period of reduced deer densities during the 1990's (Pulsifer and Nette 1995). Although moose populations declined after deer range expansion into northwestern Ontario in the 1920's, they briefly rebounded after deer populations were reduced 50-80% by a series of severe winters in the 1970's (Lankester 2010). In northeast Minnesota, point estimates of moose have remained stable since 2014, which seems to correspond with reduced deer densities following the severe winters of 2012-2013 and 2013-2014 (DelGiudice 2017).

In contrast, when either deer or gastropod secondary hosts are absent along the southern edge of moose range, moose density can be an order of magnitude higher than in other areas of their range where deer and gastropods are present. Two examples of moose reaching high population densities in the absence of deer are Isle Royale National Park

and Newfoundland. Density of moose on Isle Royale has fluctuated from < 1 to > 4 moose / km^2 since the early 1900's, with and without the presence of wolves (*Canis lupus*) (Vucetich and Peterson 2004). Newfoundland had densities of < 1 to > 5 moose / km^2 in the absence of deer and wolves (McLaren and Mercer 2005). Unlike on Isle Royale, wolves were extirpated from Newfoundland in the early 1900's, and hunting is the primary cause of mortality for adult moose (McLaren and Mercer 2005). Higher densities of moose in regions where deer and their associated parasites are absent is consistent with the hypothesis that parasite-mediated competition prevents moose from reaching high densities when deer and *P. tenuis* are present. Despite evidence for parasite-mediated competition based on several observations of an inverse relationship between deer densities and moose population declines, it has been difficult to define the underlying mechanism of disease transmission between deer and moose, specifically whether the moose-deer-*P. tenuis* system is frequency or density dependent.

Where deer and moose ranges overlap, and *P. tenuis* is present, a density threshold of <5 deer / km^2 has been recommended for moose persistence (Karns 1967, Whitlaw and Lankester 1994, Lankester 2010). However, there has been only one attempt to quantitatively test whether there is a significant negative relationship between deer densities and moose densities. The threshold hypothesis was tested by Whitlaw and Lankester (1994), when they analyzed data on moose densities and deer densities from Wildlife Management Units (WMU's) in Ontario. Their conclusion was that deer had a negative impact on moose populations when deer densities exceeded 4 deer / km^2. Their conclusion was based on fitting a third order polynomial to data on moose and deer population densities. However, moose density was high in some WMU's when deer were

present and above the threshold, and low in some WMU's where deer were absent. This result was partially explained by deer only being present on the southern edges of WMU's because of winter severity, and forage productivity limiting moose densities to the north (Whitlaw and Lankester 1994).

Whitlaw and Lankester's (1994) initial analysis of the potential relationship between moose and deer densities illustrates the complexity of the question. Although their third order polynomial relationship between deer population density and moose population density was statistically significant, it only explained about 15% of the variation (Whitlaw and Lankester 1994). The data set contained apparent outliers and influential points that could lead to misinterpretation of the results and incorrect inferences about the threshold density of deer that might negatively impact moose populations.

Additionally, density dependent disease transmission typically results in linearly increasing prevalence and so we would expect the relationship between deer densities and moose densities, when gastropods are also present, to be linear as well (Begon et al. 2002). If transmission is frequency dependent, then we would not expect a relationship between deer densities and moose densities (Begon et al. 2002). If transmission is to some degree both density dependent and frequency dependent, then there may be a non-linear relationship, though the trend should still be increasing prevalence and declining moose populations with increasing deer densities or increasing contact rates between moose and deer (Fenton et al. 2002). None of these potential disease transmission relationships would be best represented by a third order polynomial.

These issues led us to reanalyze the dataset using additional regression types. Our objective was to determine whether we could improve upon the model from Whitlaw and Lankester (1994) to gain a better understanding of moose-deer population dynamics where *P. tenuis* is a disease risk to moose. We examined the Whitlaw and Lankester (1994) dataset for outliers and refit models with outliers removed to test whether model fit could be improved, and whether inferential power could be increased.

Methods

We first digitized Figure 2 from Whitlaw and Lankester (1994) to recreate the moose and deer density dataset. The dataset included estimates of deer and moose densities from 53 WMU's across northwest and southern Ontario. The initial model relating moose density (moose/km^2) to deer density (deer/km^2) used by Whitlaw and Lankester (1994) was a 3rd order polynomial regression model. We evaluated several alternative candidate models, including simple linear regression, 2nd order polynomial regression, and negative binomial regression, with and without statistical outliers.

We used the chi-squared test in program R (R Core Team 2016) using package 'outliers' (Komsta 2011) to test for statistical significance of outliers. We sequentially removed groups of outliers from the analyses, starting with statistically significant outliers and then removing visually identified influential points to test whether predictive power could be improved with a simple linear regression and 2nd order polynomial regression. Because several WMU's had deer densities near zero, we also performed a negative binomial regression along with a likelihood ratio test to assess the value of including a deer density parameter in the model. Models were compared using

coefficient of determination (R^2) values and the corrected Akaike Information Criterion (AICc) for small sample sizes.

Results

It was not possible to associate all values from Figure 2 with additional spatial meta-data presented in Table 1 in Whitlaw and Lankester (1994). Spatial meta-data (i.e., geographic coordinates) in Table 1 included WMU's that correspond to those used to obtain density estimates but had more than 53 values for moose and was missing values for some deer density estimates. Consequently, we were unable to attribute points in the figure with WMU location and could not examine the spatial distribution of density estimates and how deer densities might relate to latitude using WMU's.

The first outlier initially identified was a moose density of 0.2 moose/km^2 and a deer density of 9 deer/km^2. The second group of outliers visually identified were moose densities of > 0.50 moose/km^2. The data point at 1.1 moose/km^2 and 2.25 deer/km^2 was a statistically significant outlier (X_2^2 = 19.13, $p < 0.01$), as was the moose density of 0.2 moose/km^2 at a deer density of 9.2 deer/km^2 (X_2^2 = 10.87, $p < 0.01$). The third group of potential outliers included four points with moose densities > 0.5 moose/km^2. Values in the second and third group visually identified as potential influential points were not statistically significant outliers (X_2^2 = 1.22, $p = 0.26$).

Polynomial regression models did not improve with removal of statistical outliers or influential points because P-values were not significant and R^2 values actually decreased (Table 1.2, Figure 1.1). Two of the models (the replication of the Whitlaw and Lankester regression, and 2nd order polynomial with statistical outliers removed) were significant at $\alpha = 0.05$ (Table 1.2). There was no significant relationship when influential

points (n = 2 and n = 6) were removed for any other models (Table 1.2, Figure 1.1). The AIC_c values indicate best models were a 2nd order polynomial regression that included statistical outliers (AIC_c = -18.73), and a linear regression excluding statistical outliers (AIC_c = -18.74; Table 1.2). Less than 20% of variability was explained by any model, regardless of inclusion or removal of potential outliers. The negative binomial regression model was not significant (p = 0.19). Including deer density as a parameter in the negative binomial regression model was also not significant (p = 0.21).

Discussion

Although the logic of an inverse relationship between deer and moose densities because of parasite-mediated competition seems sound, 50 years after Karns (1967) suggested a deer density threshold and 25 years after Whitlaw and Lankester (1994) empirically tested for a deer density threshold, we still do not have population datasets of sufficient size, precision, or accuracy to statistically support the hypothesis that moose population size is negatively related to deer density. The variability in moose population density explained by deer density in the regression models we fit was within the margin of error of any population estimate made for moose (DelGiudice 2017). In our reanalysis, using additional regression types that are more appropriate for density dependent transmission mechanisms, and removing highly influential outlier points, it was clear that despite qualitative and semi-quantitative observations (Lankester 2010), the hypothesis of declining moose densities caused by correspondingly high deer densities is not supported by the data presented in Whitlaw and Lankester (1994).

Since the 1900's, moose population declines have been documented from Nova Scotia and New Brunswick to Minnesota and northwestern Ontario, Canada (Murray et

al. 2006, Lankester 2010). High levels of *P. tenuis* infections in moose as a result of high deer densities has often been implicated as a significant factor in these declines. A qualitative analysis of these declines identifies *P. tenuis* infection, as a result of high deer densities, as the most probable cause (Lankester 2010). However, evidence for a statistically significant relationship between high deer densities and lower moose populations remains equivocal, and whether transmission of *P. tenuis* is driven by density dependence, frequency dependence, or both is uncertain.

Lack of statistical significance in tests attempting to link moose population declines to *P. tenuis* and deer may be an example of a Type II error, where the probability of falsely inferring the absence of a relationship may have been exacerbated because of uncertainty in estimating population densities, small sample sizes of moose with *P. tenuis*, and moose population declines that extend over a decade. Additional complicating factors vary by location and include differences in weather, changes in habitat, the presence and abundance of predators, and the presence and abundance of other parasites that can impact moose health (e.g., *Fascioloides magna* and *Dermacentor albipictus*, Samuel 2004, Murray et al. 2006). Liver flukes, for example, are trematode parasites of deer and moose, and have been implicated in moose population declines (Murray et al. 2006). However, despite marked infections found in some moose livers evidence that liver fluke infection can cause mortality in moose is limited (Lankester 2010, Wünschmann et al. 2015). Winter ticks are an external parasite of moose that can cause mortality. Moose are susceptible to mortality from winter ticks because large infestations can lead to anemia (Wünschmann et al. 2015) and hair loss from grooming (Samuel 1991), which can lead to hypothermia (Glines and Samuel 1989). The prevalence of

internal and external parasites is likely to increase in moose range as a consequence of climate change, either by range expansion and increased deer densities or by increasingly hospitable environmental conditions for parasites.

While the third-order polynomial regression model used by Whitlaw and Lankester (1994) predicted a significant decline of moose densities as deer densities increase above 4/km^2, Whitlaw and Lankester (1994) recognized the limitations of the dataset. Despite the authors' acknowledgement that the results provided weak inferential power, the specific threshold that they identified is often used as a benchmark for managing deer in sympatric range. A Google Scholar search identified 36 citations of the Whitlaw and Lankester (1994) paper referencing the deer population threshold, but that number alone is likely an underestimate of the impact of their paper. State natural resources agencies have referred to maintaining deer densities at the Whitlaw and Lankester threshold in non-peer reviewed literature such as moose management plans (e.g., Minnesota Moose Research and Management Plan, 2011), and related documents pertaining to moose management.

The threshold hypothesis states that there is a population density of deer below which the disease cannot persist at high enough levels in the environment to be a significant threat to moose (Schmidt and Ostfeld 2001). While Whitlaw and Lankester (1994) suggest that the threshold is 4 deer/km^2, deer densities within moose range in Minnesota have never exceeded 4 deer/km^2 (D'Angelo and Giudice 2016). Yet, since the beginning of Minnesota's cause-specific moose mortality project in 2013 approximately 30% of moose deaths were attributed to parasites, primarily *P. tenuis* (M. Carstensen,

pers. comm), while deer densities in the region have been the lowest observed in over a decade (D'Angelo and Giudice 2016).

While the management goal cited by Whitlaw and Lankester (1994) has served as a general rule for moose management, additional biological support for managing deer densities for the benefit of moose is needed. Given the poor support for the threshold deer density identified by Whitlaw and Lankester (1994), we are unable to assess whether management efforts to keep deer densities below threshold values have benefitted moose. Additionally, relying on a poorly supported threshold may also have resulted in management agencies overlooking other factors that could be significant drivers of moose population declines but that may be more difficult to detect. For example, that we found no evidence of a density dependent relationship between moose and deer populations where *P. tenuis* infection is a risk factor may imply a frequency dependent disease transmission mechanism. If the disease transmission mechanism in the moose-deer-*P. tenuis* system is frequency dependent, this would indicate that contact rates between deer, moose, and gastropod hosts are more important drivers of disease transmission than deer density alone. Therefore, if this is a frequency dependent system, management efforts that aimed only to keep deer densities low within moose range would have been insufficient to prevent *P. tenuis* transmission from deer to moose.

Management decisions could benefit from research that elucidates more completely the dynamics of the moose-deer-snail-parasite-habitat relationship. Focusing solely on the density dependence requirement for disease transmission from deer to moose does not provide information about whether habitat partitioning exists between moose and deer on sympatric range. Understanding similarities in the use of resources

between moose and deer could shed light on how the contact rates between species might be influenced by parts of the landscape that are either mutually selected or mutually avoided by moose and deer.

In Minnesota, ≥70% of deer are infected with *P. tenuis* (Peterson et al. 1996, Gogan et al. 1997, Vanderwaal et al. 2015). Both moose and deer acquire *P. tenuis* by incidentally consuming any of several species of terrestrial gastropods and a few aquatic gastropods (Lankester and Anderson 1968). *P. tenuis* larvae are generally present in < 0.5% of gastropods (Lankester and Peterson 1996). To date, the likelihood of moose and deer ingesting infected gastropods has been explained by the fact that deer and moose eat large quantities of vegetation, and therefore despite the low incidence of infection in gastropods, some moose and most deer will still become infected through incidental ingestion of many snails (Lankester 1967).

Moose population declines, if caused by *P. tenuis*, would necessarily occur only if moose forage in areas where deer defecate and where gastropods occur. Therefore, biological questions remain about how and when resources are used by moose and deer, and in what biologically significant ways moose are at high risk of becoming infected. Specifically, does moose distribution overlap with deer presence at a time of year when *P. tenuis* larvae are most prevalent and developed to infective stages in gastropods? How often and when does the overlapping distribution of moose and deer occur in areas that provide forage and therefore a potential route of infection? This can be tested using fine-scale location data of moose and deer to determine resource use for each species and to identify riskier portions of landscape for moose. We propose that analyzing interactions between deer and moose in terms of resource selection on sympatric range may provide

novel insights into questions related to moose-deer-parasite dynamics and to whether parasite-mediated competition may contribute to declining moose populations.

Table 1.1. *Parelaphostrongylus tenuis* infection rates reported in deer sympatric with moose in North America. With the exception of Saskatchewan and western North Dakota, deer infection rates were high regardless of reported deer densities.

Region	Deer infection rate	Deer/km^2	Author	Year
New Brunswick	60%	Not reported	Upshall	1987
Maine	73%	<1-2	Bogaczyk	1993
Maine	84%	Not reported	Behrend and Witter	1968
Maine	63-80%	1-6	Gilbert and Frederick	1974
Quebec	63%	Not reported	Bindernagel and Anderson	1972
UP Michigan	44%	3-7	Nankervis	2000
Ontario	63%	Not reported	Bindernagel and Anderson	1972
NW Ontario	47%	4-5	Saunders	1973
NW Ontario	58%	0-9	Whitlaw and Lankester	1994
NE Minnesota	82%	12	Slomke	1995
NE Minnesota	69%	2	Vanderwaal et al.	2015
C. Minnesota	69%	12	Karns	1967
N. Minnesota	39%	4-6	Karns	1967
Manitoba	49%	Not reported	Bindernagel and Anderson	1972
North Dakota	14.5% (range: 1-35%)	Not reported	Maskey et al.	2015
Saskatchewan	9%	Not reported	Bindernagel and Anderson	1972

Table 1.2. Relationship between moose density (moose/km^2) and deer density (moose/km^2) as presented in Whitlaw and Lankester (1994), and additional candidate models we tested. The relationship was only significant when using a second- (this study) or third-order (Whitlaw and Lankester 1994) polynomial model. For the former, this was true only when two statistical outliers were removed.

Regression	Outliers (Included/Excluded)	DF	Adjusted R^2	p-value
3rd Order Polynomial	Included	3	0.16	0.02
	Excluded 2	3	0.06	0.12
	Excluded 6	3	<0.001	0.40
2nd Order Polynomial	Included	2	0.01	0.33
	Excluded 2	2	0.08	0.05
	Excluded 6	2	0.003	0.35
Linear Regression	Included	1	0.01	0.20
	Excluded 2	1	0.02	0.16
	Excluded 6	1	0.02	0.15

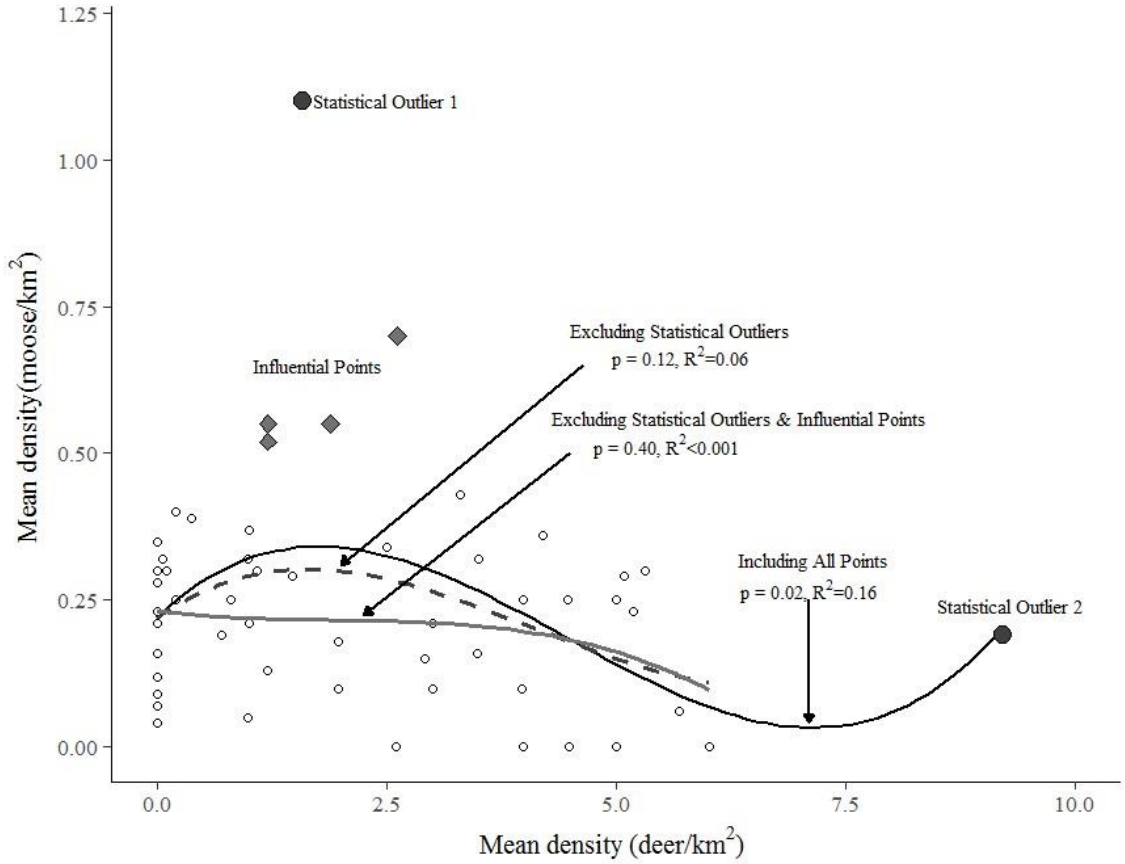


Figure 1.1. Third order polynomial regression model provided by Whitlaw and Lankester (1994) as part of their analysis relating moose to deer densities in Ontario, Canada. The solid black line is the original 3rd order polynomial regression line as presented in Whitlaw and Lankester (1994). We refit the model by excluding two statistical outliers. An additional four points were identified as influential, and so we removed those points and refit the model again. In each iteration model fit and statistical significance was reduced, and no relationship was found between moose and deer densities in this dataset.

Chapter 2

Seasonal resource selection by migratory and non-migratory white-tailed deer in northeast Minnesota

Preface

While the importance of winter deer yards and migration has been recognized for decades in partially migratory populations, differences between winter and summer space use and resource selection by migratory and non-migratory deer in the same populations have received less attention. We tracked deer (N = 53) with global positioning system (GPS) radio collars in northeast Minnesota from December 2013 to November 2015 to determine migratory strategy and to characterize differences in seasonal space use, movement, and resource selection by migratory and non-migratory deer. The percent of migratory deer in our study (35%) is a significant departure from previous reports that approximately 80% of deer in northeast Minnesota are migratory. We found that migratory deer had significantly larger home ranges than non-migratory deer during the summer while home range sizes were similar between migratory and non-migratory deer in winter. During the winter, movement by deer was negatively related to increasing snow depth. There were no significant differences in land cover composition within home ranges between migratory and non-migratory deer in winter. However, non-migratory deer had more shrub land cover available than migratory deer in summer home ranges. Migratory deer showed a stronger selection for the shrub and mixed forest cover types in summer. Taller, sparser canopied forests with denser understories were also more strongly selected by migratory deer in the summer, compared to non-migratory deer. Differential patterns of space use and resource selection by migratory and non-migratory deer in partially migratory populations could be important when considering the direct impacts deer have on vegetation. The apparent decline in the number of migratory deer in the region, and potential causes for that decline, should be investigated.

Key words: migration, Minnesota, *Odocoileus virginianus*, resource selection, white-tailed deer

Introduction

Many white-tailed deer (*Odocoileus virginianus*) in northern populations are migratory or occupy distinctly seasonal home ranges, though a portion of deer in northern populations are non-migratory and remain on the same home range throughout the year. Between 50-85% of deer are migratory in any year in northern Minnesota (Pierce 1975, Nelson 1997, Fieberg et al. 2008). The proximate reason for migration to winter ranges is avoidance of deep snow and the associated energy cost of locomotion (Verme 1968, Drolet 1976). Yarding together on winter ranges also serves as an anti-predation strategy where congregations of deer at high densities leads to the establishment of trail systems that act as escape terrain and increased sensory warning systems (Nelson and Mech 1981, Messier and Barrette 1985, Nelson and Mech 1991).

For deer populations in northern portions of their range, climate exerts the greatest influence on seasonal patterns of movement and space use (Verme 1968, Tierson et al. 1985). Deer populations at more southern latitudes with mild winters are non-migratory and occupy annual home ranges (Sparrowe and Springer 1970), while deer in northern latitudes with severe winter conditions often migrate between summer and winter ranges each year (Van Deelen et al. 1998, Fieberg et al. 2008). Fall migration behavior may be induced by a variety of weather conditions such as snow depth, low temperatures, and reduced photoperiod where winters are consistently severe (Nelson 1995, Sabine et al. 2002). In northern regions where winter severity is more variable, snow depth appears to be the driving factor that triggers fall migrations (Sabine et al. 2002). In contrast, spring migration is consistently linked to the loss of snow cover regardless of which factors influenced fall migration (Nelson 1995, Sabine et al. 2002).

Among migratory deer, two types of migratory behavior have been described. Obligate migrators move between ranges each season regardless of winter weather conditions, whereas conditional migrators move to winter ranges only when weather conditions, primarily snow depth, dictate. Conditional migrators may also migrate temporarily within a season in response to specific weather events (Nelson 1995, Sabine et al. 2002, Brinkman et al. 2005). Despite variability in migratory strategy and seasonal space use, analyses of seasonal resource selection by northern deer do not often explicitly differentiate between migratory and non-migratory deer, either lumping them together or focusing only on resource selection by migratory deer between seasons.

An implicit assumption is that despite differences in seasonal movement patterns and space use, variance in migratory behavior does not correspond with variance in patterns of seasonal home range habitat composition or resource selection within home ranges. However, recent studies suggest that landscape characteristics such as forest patch size and patch density may influence migratory strategy in deer (Grovenberg et al. 2011), and non-migratory deer may have higher quality home ranges than migratory deer (Henderson et al. 2018). This implies a difference in available resources and resource use between migratory and non-migratory deer within seasons.

In northern latitudes, deer mortality is predominately due to hunting, predation, and winter starvation. Understanding the winter ecology of deer in northern populations is critical because overwinter survival of deer has a large impact on population size. More than 80% of all adult deer mortality occurs between November and May (DelGiudice et al. 2002), and in severe winters, about 25% of the adult deer and 50% of fawns may die from starvation and predation (Kohn 1975), which is primarily related to snow depth

(DelGiudice et al. 2002). Migratory deer that winter in deer yards have up to nine times higher survival rates than non-migratory deer that spend winter outside of yards (Nelson and Mech 1991, Nelson 1995).

Deer yards typically have a coniferous forest component, usually dense spruce or cedar, that offers thermal cover. Young regenerating mixed forests or deciduous forest stands with available forage are often found adjacent to thermal cover at winter yards (Tierson et al. 1985, Van Deelen et al. 1998). Trail systems established by deer movements through the snow in winter yards reduce travel costs and increase access to forage and thermal cover (Telfer and Kelsall 1984, Messier and Barrette 1985), and aid escape from predators (Nelson 1995).

Relative deer density changes seasonally as deer migrate to winter yards and disperse to summer ranges, which likely leads to differential impacts on vegetation on winter and summer ranges. Deer density can exceed 80 deer/km^2 in winter deer yards along the shore of Lake Superior in northeast Minnesota, while densities in winter deer yards inland are between 14-24 deer/km^2 (Nelson and Mech 1987). Repeated use of deer yards in winter gradually leads to the elimination of preferred forage species such as tree species in the white pine-hemlock and northern hardwood forest communities (Waller and Alverson 1997), the reduction of plant diversity and the prevention of regeneration of commercial tree species important to the timber industry (Verme and Johnston 1986, Alverson et al. 1988, White 2012).

The summer ecology of deer in northern latitudes is less understood than winter ecology, despite the documented impacts deer can have on the habitat through summer browsing and the importance of summer habitat on fecundity and productivity

(McCaffery and Creed 1969, Verme 1969). Woody species can constitute 68% of summer deer diets in northern forests (Kohn and Mooty 1971) where browsing has a greater adverse effect on plant growth than browsing in winter because in summer metabolically active meristems and photosynthetically active tissues are consumed (Bradshaw and Waller 2016).

Deer also have a higher degree of fidelity for summer home ranges than for winter home ranges (Verme 1973, Tierson et al. 1985, Van Deelen et al. 1998). Social factors rather than habitat type appear to dictate establishment of summer home ranges (Tierson et al. 1985). Habitat is used in proportion to availability during the summer (Kohn and Mooty 1971), which implies that resources such as forage and cover are not as limiting during summer as they are in winter. We propose that because of the documented impact deer can have on northern forests through summer browsing, that an increased understanding of summer space use and resource selection will improve management of deer in areas where they are having a negative impact on the local plant community.

We used Global Positioning System (GPS) radio telemetry to study seasonal resource selection by deer in northeast Minnesota. Our objectives were to determine 1) whether there was differential resource selection between non-migratory deer and migratory deer within a season, and 2) whether there was differential resource selection between non-migratory and migratory deer between seasons.

Study Area

We conducted this study in northeast Minnesota, USA (Figure 2.1). Deer were captured at two locations within the study area. The Ely site (960 km^2, centered on latitude: 47° 52’ 55.2” N, longitude: 91° 59’ 16.8” W) is in deer permit area (DPA) 118,

which has had consistent density estimates of about 2 deer/km^2 since 2010 (MN DNR 2015, Figure 2.1). The Isabella site (570 km^2, centered on latitude: 47° 37' 30" N, longitude: 91° 24' 57.6" W) is in DPA 131. Deer density is assumed to be ~1 deer/km^2 at the Isabella site (MN DNR, 2015). More accurate deer density estimates are not available for DPA 131 due to low hunter harvest rates. Primary predators of deer in northeast Minnesota are wolves (*Canis lupus*) and American black bears (*Ursus americanus*) (Kunkel and Mech 1994). Deer are harvested annually in the fall during archery and firearms seasons (D'Angelo and Giudice 2016).

The region is classified as sub-boreal, with latitudinal transition from northern hardwood forests to the south to boreal forests to the north (Pastor and Mladenoff 1992). Coniferous forests consist of white pine (*Pinus strobus*), red pine (*P. resinosa*), jack pine (*P. banksiana*), and balsam fir (*Abies balsamea*). Upland deciduous forests are typically aspen (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Lowland forests are predominately northern white cedar (*Thuja occidentalis*), tamarack (*Larix laricina*) and black spruce (*Picea mariana*), with occasional lowland hardwood stands dominated by black ash (*Fraxinus niger*, Minnesota Ecological Classification System 2008).

Summers are typically warm with an average maximum July temperature of 26°C (National Oceanic and Atmospheric Administration [NOAA] 2015). Winters are moderate to severe and snow cover is typically present from December to April, with annual snowfall regularly reaching 180-cm. The average low temperature in January is -21.5°C (NOAA 2018). A winter severity index (WSI) is calculated between November 1 and May 30 each year by accumulating a point for each day that ambient temperatures are ≤ -17.8°C (0°F) and a point for each day that snow depths exceed 38-cm (15-in.,

DelGiudice et al. 2002). WSI values < 120 at the end of winter correspond to a mild winter while WSI values > 180 indicate severe winters. The WSI was >180 during winter 2013-2014 and <120 during winter 2014-2015 (Minnesota Winter Severity Index, 2014 & 2015).

Methods

Habitat variables metadata

We characterized deer habitat using different sources of remotely sensed data; coarse landcover data from the National Land Cover Database (NLCD) and finer Light Detection and Ranging (LiDAR)-based metrics of forest structural components. Land cover types were extracted from the 2011 NLCD (Homer et al. 2015). The NLCD is a remotely sensed dataset of land cover created from Landsat Thematic Mapper imagery with 30-m spatial resolution. Sixteen land cover types are defined in the NLCD dataset. Each of the forested land cover types are defined as having >20% vegetation cover within the 30-m pixel (Homer et al. 2015). There are three forested cover types that are likely to be the main foraging habitat for deer; deciduous forest, mixed forest, and shrub stands (Table 2.1). Deciduous forests have canopies consisting of >75% deciduous trees and are 20% of the study area. Shrub stands are >75% either true shrubs or young deciduous trees, or some combination of both, and are 14% of the study area. Mixed forest stands make up 16% of the study area and have canopies that are no greater than 75% of either deciduous or coniferous trees. The coniferous forest cover type is considered an important thermal cover for deer in winter in the region (Nelson 1995, DelGiudice et al. 2013) and has a canopy that is >75% evergreen and is 16% of the study area. The woody wetlands cover type is either wet forest or wet shrub with soils that are periodically

saturated or covered with water and is 22% of the study area. Other NLCD land cover types such as development, hay/pasture, and emergent wetlands are each <5% of the landscape. We combined land cover types that constituted <5% of the study areas into a single category called "other", which summed to 5% of the landscape, because they constituted a negligible portion of the landscape and are cover types that are likely of limited value to deer. Because the area is not agricultural, we believe that land cover categories such as hay/pasture are categorized incorrectly, and that emergent wetlands act more as barriers to deer than as accessible habitat.

We used LiDAR data to characterize forest structural heterogeneity across the landscape. LiDAR data was collected over the entire study area during leaf-off conditions in May 2011 (Minnesota Geospatial Information Office, 2015). Data met National standards for accuracy (Federal Geographic Data Committee 1998) with a vertical accuracy RMSE of 5.0-cm and a horizontal accuracy of 1.16-m. Discrete returns resulted in point clouds representing vegetation and land surfaces. Total height of returns above ground was calculated by subtracting the height of the LiDAR-derived Digital Elevation Model (DEM) from the height of points. The 75^{th} percentile of canopy height was used to represent the heights of dominant trees and to reduce the potential influence of super-canopy white pine within mixed and conifer forests. Canopy vegetation density was the proportion of non-ground returns above 3-m. The proportion of non-ground returns above 1-m and below 3-m was used to index understory vegetation density. LiDAR-derived metrics of habitat structural heterogeneity were averaged within 30 x 30-m pixels within the study area.

Animal capture and telemetry

Adult deer, yearling deer, and female fawns were captured using collapsible Clover traps (Clover 1956), physically restrained, blindfolded and chemically immobilized with a combination of 100-mg xylazine HCl and 300-mg ketamine HCl injected intramuscularly via handheld syringe (DelGiudice et al. 2005). Male fawns were immediately released from traps after sex and age was determined, without immobilization or blindfolding.

Deer were fitted with GPS radio collars (GPS PLUS Vertex Survey Iridium, Vectronic Aerospace GmbH, Berlin, Germany). We collected blood, hair, and fecal pellets from each deer. One incisiform canine was extracted for age determination by cementum annuli (Nelson 2001). Morphological measurements taken included chest girth, hind leg length, neck circumference, and total body length. All deer received 6.7-mL broad spectrum antibiotics (LA 300) by intramuscular injection and 2.7-mL Vitamin E by subcutaneous injection. We reversed anesthesia with intravenous or intramuscular injection of 200-mg Tolazoline or intramuscular injection with 200-mg Atipamezole. Animal capture and handling protocols met American Society of Mammalogists recommended guidelines (Sikes et al. 2011) and were approved by the University of Minnesota Animal Care and Use committee (Protocol Number: 1309-30915A).

Collars were programmed to record locations every 2 hours with an expected battery life of 2 years. We retained GPS locations with 3-D fixes or 2-D fixes with dilution of precision values ≤ 5 (Lewis et al. 2007, Bjørneraas et al. 2010). Locations that were not biologically possible were removed by identifying a set of three locations where the distance from the fist location to the middle location and back to the last location

would have exceeded the maximum speed of a running deer (45-km/hour, Hewitt 2011). Deer were excluded from seasonal analyses if there was < 30 days of location data available within a season. This occurred either when a deer died or when a collar failed.

Seasonal movement patterns

We defined migration as movement between seasonal home ranges, where seasonal home ranges were disjunct from one another. We segmented locations into spring/summer/fall (hereafter summer) and winter seasonal categories based on onset of migration and arrival at seasonal ranges by migratory deer and changes in seasonal movement rates by non-migratory deer.

We used Net Squared Displacement (NSD) and changepoint analysis to identify seasonal changes in movement patterns using GPS data points from migratory and non-migratory deer, and to define the start and end of seasons. Movement by migratory and dispersing animals is often tracked by calculating the NSD for a series of sequential GPS points from radio collared animals (Dettki and Ericcson 2006). Squared distances are used to remove directional information (Bunnefeld et al. 2011, Papworth et al. 2012), and increasing values indicate movement further from a central place. We used the location of capture as the central place within winter home ranges. Homogeneous segments indicated localization at a central place (i.e. range residence during the winter) or localization at a maximum location (Papworth et al. 2012), which represented range residence during the summer.

Break points in homogeneous segments of NSD data that indicated migration from one range to another were identified using the Pruned Exact Linear Time (PELT) change point detection algorithm in Package Changepoint in Program R (Killick and

Eckley 2012 & 2013; Package: changepoint, R. Killick and Eckley, 2014). Change points were identified with the PELT algorithm by recursively iterating through the NSD data and identifying locations where changes in mean and variance were detected. Change point locations represent the start or end of a homogeneous segment of GPS locations (Figure 2.2). If no change points were detected, deer were categorized as non-migratory. If a deer was non-migratory, we partitioned data into winter and summer based on differences in step length (the distance between consecutive GPS points), which we predicted would correlate with loss or gain of deep snow. The relationship between step length and snow depth was explored using simple linear regression.

For non-migratory deer, we used the PELT algorithm and change point analysis (Killick and Eckley 2012 & 2013; Package: changepoint, R. Killick and Eckley, 2014) to test for changes in mean and variance of step lengths. If we could not detect a change in movement patterns that indicated a clear seasonal transition with the PELT algorithm, we partitioned locations into winter and summer using the average seasonal start date based on migration date of migratory deer and the date step lengths changed for non-migratory deer. We tested for differences in migration distance between years using Analysis of Variance (ANOVA). Migration distance was the shortest distance between edges of 95% kernel density seasonal home range boundaries. We tested for differences in step length by season using ANOVA.

For each animal, we delineated seasonal home ranges by calculating 95% bivariate normal kernels using the reference bandwidth (Package adehabitatHR, Program R; Calenge 2006). Calculation of seasonal home ranges for migratory deer excluded locations obtained during migration. Locations used for seasonal home range calculations

for non-migratory deer were based on average season start and end dates of migratory deer. We tested for differences in seasonal home range size using ANOVA.

Resource selection modeling

We determined resource selection using a Resource Selection Function (RSF) and a type III design where available resource units are measured at the individual level within a home range (Manly et al. 2002). We used seasonal home ranges as bounding areas for random points generated for within-home-range level of analysis. Used points were identified by GPS collar locations from each individual. We generated one random point for each used point within each seasonal home range (Manly et al. 2002, Thomas and Taylor 2006, Laforge et al. 2015).

Seasonal RSFs for migratory and non-migratory deer were estimated with logistic generalized linear mixed models using the 'glmer' function in the lme4 package (Bates et al. 2015) in R (R Core Team 2016):

$$w(x) = \exp\left(\beta_{1ij}x_{1ij} + \cdots + \beta_{nij}X_{nij} + \gamma_{0\mathrm{j}}\right)$$

where $w(x)$ is the relative probability of use, B_i are the log odds coefficient values and γ_j is the random intercept for individual animals (n designates the covariate, i designates the observation, and j designates the group (Gillies et al. 2006)).

We fitted RSF models for each season and migratory strategy separately. Individual animals were treated as a random effect in each model to control for unequal sampling and individual variability. Data were rarified to 20% of the full dataset by retaining every 5th data point. Explanatory variables included LiDAR derived metrics of canopy height variability (standard deviation of canopy height), vegetation density at two strata (vegetation density above 3-m and vegetation density between 1-m and 3-m), and

land cover type. Continuous covariates were *z*-transformed. The woody wetland cover type was used as the reference category for the land cover covariate in all models because it constitutes a large portion of the study area and because one habitat type in the categorical land cover variable is required to be removed because of dummy variable coding (Boyce et al. 2002).

We checked explanatory variables for collinearity by screening for high variance inflation factors (VIF > 5, Lewis et al. 2007, Bjørneraas et al. 2010). Two LiDAR derived explanatory variables, canopy height and standard deviation of canopy height, were highly collinear. Standard deviation of canopy height was removed while canopy height was retained in candidate models. All analyses were conducted in R (R Core Team 2016), using the lme4 package (Bates et al. 2015) to run logistic generalized linear mixed models.

The top model was selected from a set of *a priori* candidate models (Table 2.2) for migratory and non-migratory deer during each season based on Akaike's Information Criteria (AIC). A 5-fold k-fold cross validation with Spearman Rank Correlation was used to determine the goodness of fit of the top model identified by AIC (Boyce et al. 2002, Weins et al. 2008) for each season and for migratory status of deer. Regression coefficients were considered significant if 95% confidence intervals, calculated from the model coefficients and standard error estimates, did not overlap zero.

Results

We radio collared 53 deer (41 adult females, 7 females < 2-years, and 5 adult males) during winters 2014 (n = 32) and 2015 (n = 21). Twenty-five deer were collared at the Ely study site and 28 deer were collared at the Isabella study site. There was an

average of 1,180 (SE = 117) locations per deer in winter (n = 27), and 1,825 (SE = 84) locations per deer in summer (n = 38). Failed fix attempts, removal of locations with 2-D and 3-D DOP > 5, and removal of locations where distances traveled were not biologically reasonable resulted in the loss or removal of 6% of GPS locations during winter and 10% of GPS locations during summer.

The mortality rate of collared deer during the severe winter of 2013-2014 was 30%. Starvation was the cause of death for four deer, and six were either killed or scavenged by wolves. The mortality rate was 5% during the mild winter of 2014-2015. Two radio collared deer were apparently predated by wolves in winter 2015, and no starvation deaths were documented. All mortalities during summer each year were attributed to apparent predation by wolves (two in 2014 and three in 2015). One male deer was legally harvested during the 2015 firearms deer season. We documented no instances of radio collared deer dying during migrations.

Seasonal movement patterns

In our study 35% of deer were migratory and 65% of deer were non-migratory (Table 2.3). Similar proportions of deer were migratory at the Ely and Isabella study sites, and migratory deer and non-migratory deer were captured together at study sites with some overlap of winter home ranges between groups. Deer migration to winter yards took place before snow depths reached the WSI threshold of 38-cm in early winter and then took place again in the spring when deer moved to summer home ranges when snow depths receded to below 38-cm Figure 2.2). The mean spring migration date was 23 April at the Ely site in 2014 and 2015. The mean spring migration date at the Isabella site was 28 April in 2014 and 19 April in 2015. Fall migration began at the end of November and

extended to mid-December (Table 2.3). Migratory deer at each study site traveled similar distances between winter and summer home ranges in each year ($p = 0.263$, $F_{1,25} = 1.33$, Figure 2.3). Deer migrated 7.4 ± 0.97-km between winter and summer ranges (Table 2.3). No differences were detected in deer home range size between study sites during the summer ($\overline{X}$: 1.85-km^2 ± 0.32-km^2) or winter ($\overline{X}$: 1.75-km^2 ± 0.37-km^2; $F_{1,77} = 0.21$, $p = 0.65$, Table 2.3). There were no differences in winter home range sizes between migratory and non-migratory deer ($F_{1,42} = 0.31$, $p = 0.58$, Table 2.4), but home ranges of migratory deer were significantly larger than home ranges sizes of non-migratory deer in the summer ($F_{1,42} = 11.48$, $p = 0.001$, Table 2.4).

Deer movement within home ranges was seasonally dependent. Mean step lengths during winter were 99-m/2-hr (SE ± 7-m/2-hr), which were significantly shorter ($F_{1,77} = 31.82$, $p < 0.001$) than the average step lengths in summer (147-m/2-hr, SE ± 5-m/2-hr). Step lengths in winter were inversely correlated with snow depth ($r^2 = 0.89$, $p < 0.001$, Figure 2.4). Step lengths during winter 2013-2014 were 56-m/2-hr (SE ± 8-m/2-hr), which were significantly shorter ($F_{1,43} = 31.62$, $p < 0.001$) than the 116-m/2-hr (SE ± 6-m/2-hr) step lengths in winter 2014-2015.

Resource availability and selection

We did not observe clustering or segregation of migratory or non-migratory deer on winter ranges. Rather, winter home ranges of migratory and non-migratory deer overlapped. As such, the proportions of available habitat types within winter home ranges of migratory and non-migratory deer were similar (Figure 2.5). About 21% ± 3% of winter home ranges consisted of conifer cover, while the remainder of forested cover

types available included 16% ± 3% deciduous forest, 22% ± 3% mixed forest, 15% ± 2% shrubs, 20% ± 3% woody wetlands, and 5% ± 1% other cover types.

During summers when migratory deer moved away from winter ranges shared with non-migratory deer, we observed similar land cover type availability between migratory and non-migratory deer (Figure 2.5), with the exception of the shrub cover type. Migratory deer had significantly less shrub cover type available in summer home ranges (7% ± 2%) than did non-migratory deer (19% ± 3%, $t(19) = 3.567$, $p = 0.001$). Aside from the shrub cover type, there were no significant differences in land cover type availability between home ranges of migratory and non-migratory deer during the summer. On average, summer home ranges consisted of 18% ± 2% conifer, 18% ± 3% deciduous forest, 16% ± 2% mixed forest, 23% ± 2% woody wetlands, and 6% ± 1% 'Other' land cover types. The distribution of canopy height, canopy cover, and understory density in each cover type was similar among home ranges (Figure 2.6).

The best predictive model at the within-home-range scale for winter and summer for migratory and non-migratory deer included land cover type, canopy height, canopy cover, and understory density covariates. Cross-validation scores for top RSF models for migratory and non-migratory deer during summer indicate good fit and predictability (Table 2.6). Cross-validation scores for winter models were lower, indicating a slightly poorer model fit during winter (Table 2.6).

During the winter, the conifer cover type was used in proportion to its availability by migratory and non-migratory deer. Also, during winter both migratory and non-migratory deer selected deciduous forests, mixed forests, and shrub cover types, relative to the woody wetlands cover type, which served as a reference category (Figure 2.7).

In winter migratory deer avoided the ‘Other” land cover type while non-migratory deer used the ‘Other’ land cover type in proportion to its availability. Additionally, migratory deer appeared to have a stronger relative probability of selection than non-migratory deer for deciduous forests, mixed forests, and shrub stands in winter (Figure 2.7). The relative probability of selection for canopy height during winter was not significant in models for non-migratory deer while canopy height was a significant predictor in the winter resource selection model for migratory deer, which avoided taller canopies in winter (Table 2.7, Figure 2.8). Migratory and non-migratory deer selected for denser canopy cover and higher understory density in winter (Figure 2.8).

During the summer, migratory and non-migratory deer had similar selection patterns for land cover type, selecting for all land cover types relative to the woody wetlands reference land cover category (Figure 2.7). Differences in selection for land cover types between migratory and non-migratory deer appeared to occur in the stronger selection by migratory deer for deciduous forests, mixed forests, and shrub stands, and coniferous forests, based on non-overlapping 95% confidence limits. Migratory deer did not select or avoid forests relative to canopy height (Figure 2.9) or understory density (Figure 2.9) in the summer. In contrast, non-migratory deer selected for taller canopies and denser understories in the summer. Migratory and non-migratory deer both avoided denser canopies during the summer (Figure 2.9).

During the summers of 2014 and 2015 deciduous forests, mixed forests, shrub lands, and woody wetlands accounted for a total of 82% and 74%, respectively, of the habitat available to deer within their summer home ranges (Table 2.8) while deciduous forests, mixed forests, shrub lands, and woody wetlands made up 84% and 77% of the

habitats used by deer in summers 2014 and 2015, respectively (Table 2.8). Conifer forests made up 17% and 20% of the available habitat in summer home ranges of deer in 2014 and 2015, respectively, while conifer forests made up 15% and 17% of the used habitat by deer in summers 2014 and 2015, respectively (Table 2.8). In contrast, during the winters of 2014 and 2015 deciduous forests, mixed forests, shrub lands and woody wetlands accounted for 65% and 63%, respectively, of the habitat available to deer within their winter home ranges (Table 2.8). Deciduous forests, mixed forests, shrub lands, and woody wetlands made up 67% and 77% of the habitats used by deer in winters 2014 and 2015, respectively (Table 2.8). Conifer forests were 31% and 19% of the habitat available to deer in their winter home ranges in 2014 and 2015, respectively, while conifer forests were 33% and 18% of the habitat used by deer within their winter home ranges in 2014 and 2015, respectively (Table 2.8).

Discussion

Seasonal movement patterns

Only 35% of deer within our study area were migratory, and 14 of 15 migratory deer moved to and from winter ranges when snow depths were less than the 38-cm threshold used for calculating the WSI. Regardless of whether deer were migratory or non-migratory, movement during winter was negatively correlated with snow depth and home range sizes were similar. In contrast to winter, migratory deer occupied home ranges that were nearly double the size of non-migratory deer home ranges in the summer.

Our observation of a 35% migration rate was significantly less than the 80% of deer in northeast Minnesota that were thought to be either obligate or conditional

migrants in the past (Nelson and Mech 1987). The cause of deer migration is an important and complex question for deer management at northern latitudes. Deer are in negative energy balance during the winter because of the loss of nutritious forage and increased energetic costs of locomotion associated with deep snow (Moen 1978). Migration increases survival because when deer yard together they create trail systems that decrease the energetic cost of locomotion, making access to forage and cover easier while also increasing the probability of escaping predation (Nelson and Mech 1981, Nelson 1997).

Migration in deer is a learned behavior (Nelson 1997), and deer tend to migrate together in matrilineal groups and as associations of non-related males (Van Deelen et al. 1997). Most deer remain faithful to the migration tradition and to seasonal home ranges throughout life, but migration behavior is also flexible, and some animals will abandon migration to deer yards when weather conditions are favorable (Drolet 1976, Fieberg et al. 2008). As the frequency of severe winters declines as a result of climate change, a cohort of deer may not experience the need to migrate, contributing to a decline in the memory of migration routes and winter yard locations as older deer die and the learned behavior is not passed on to offspring.

The migration tradition is also not passed on completely, as some dispersing juvenile deer will abandon migration (Nelson 1997, Van Deelen et al. 1997). While conditional migration and abandonment of the migration tradition by offspring is influenced by weather, habitat quality could also affect the decision to migrate. The abandonment of migration by young dispersing deer could be a reflection of establishing home ranges on higher quality habitat than their natal social group. Also, changes in

summer habitat through the addition of forage resources, such as regenerating young forests as a result of recent timber harvest or natural disturbance (Van Deelen et al. 1997) can allow dispersing juveniles and conditional migrants to remain on summer ranges throughout the year.

Resource availability and selection

In northern latitudes where deer are migratory, summer home ranges are generally larger than winter home ranges (Tierson et al. 1985, Mooty et al. 1987, Nelson and Mech 1987, Van Deelen et al. 1996, Lesage et al. 2000). However, few studies have focused on the difference in home range space use and habitat selection for migratory and non-migratory deer in partially migratory populations (Henderson et al. 2018), such as the population in northeast Minnesota. There is a negative relationship between habitat quality and home range size (McLoughlin et al. 2000, Mitchell and Powell 2007), and in partially migratory populations animals with poorer quality home ranges were more likely to be migratory than individuals occupying higher quality home ranges (Henderson et al. 2018).

Our results also indicate that migratory deer may have lower quality home ranges than non-migratory deer in the summer, which could explain the larger home range size of migratory deer and differences in resource selection between migratory and non-migratory deer during summer. Differences in availability and selection for resources, paired with migratory deer occupying larger summer home ranges in areas that are vacant of deer in winter lends further evidence to the hypothesis that deer on poorer quality habitat are more likely to be migratory in partially migratory populations. Similarities in habitat availability and selection by migratory and non-migratory deer in winter may be

due to migratory and non-migratory deer occupying shared winter ranges in northeast Minnesota.

Migratory deer in our study had less of the shrub cover type available in summer home ranges than non-migratory deer, and their selection for the shrub cover type within summer home ranges was stronger than that of non-migratory deer. Migratory deer also showed a stronger selection for the mixed forest cover type than non-migratory deer during winter and summer. Selection for forest structural components also differed between migratory and non-migratory deer in the summer. Migratory deer selected more strongly for denser understories and taller canopies and avoided denser canopies more than non-migratory deer. There were no significant differences in selection between migratory and non-migratory deer for forest structural components during the winter when they occupied the same range.

Stronger selection for the shrub and mixed forest cover types by migratory deer could be an indication that if migratory deer have limited shrub stands available, they will seek out mixed forests as a less desirable alternative. Shrub habitat in northeast Minnesota includes patches of alder (*Alnus*), willow (*Salix*), and red osier dogwood (*Cornus sericea*) but can also be young regenerating deciduous stands of aspen, birch, and cherry, which are common deer foods (Crawford 1982). If shrub habitat is rich in quality forage resources, then home ranges with more shrub habitat should be higher quality.

Deer locations were collected over two years where the winters differed in severity (MN Winter Severity Index 2014 & 2015). Deer were captured after migratory deer would already have arrived on their winter home ranges, which were a matrix of

conifer, deciduous, shrub land, and woody wetland cover types (Table 2.8). Deer were captured in similar locations each year, were already on their winter home ranges, and did not use different home ranges in each winter. Winter severity can impact deer resource selection (Beier and McCullough 1990, Pauley et al. 1993, Van Deelen et al. 1997), with increasing snow depths correlating with increasing use of protective conifer cover (DelGiudice et al. 2013). In our study deer appeared to decrease movements and were more restricted to established paths through the snow during the more severe winter, 2013-2014 (McGraw, *pers. obs*.). A year effect might have been significant in the models for the conifer cover type but use of other cover types was similar relative to the woody wetland reference cover type in each year (Table 2.8). It would be beneficial for future long-term studies in the region to test for a year effect on models of resource selection, especially if there are individual deer that winter in different areas among years.

An interaction term between cover type and LiDAR-based forest structural components might also have been beneficial to include in candidate models, because there is a potential for interaction between forest structural components and cover types in terms of deer resource selection. Because we focused on differences between migratory deer and non-migratory deer, and because there was little difference in the distributions of forest structural components (Fig. 2.6), we chose to not include an interaction term. Future studies could consider a modeling approach that includes interaction terms to better elucidate how resource selection patterns are impacted by forest structural components like understory density within a cover type. For example, understory density could be similar in upland and lowland cover types, but species composition could be different. However, this approach could be affected by uncertainty

in the accuracy and composition of some cover types (Homer et al. 2015), especially uncertainty and variability in understory species composition which is not identified in the NLCD dataset.

Conclusions

Increased understanding of what is influencing deer migration and the apparently declining proportion of migrating deer in northern populations is necessary to improve deer and habitat management. Migratory and non-migratory deer have differential impacts at the landscape scale through restructuring of the vegetative community (Joly et al. 2006, Skuldt et al. 2008), and the presence of deer in summer has greater potential to structure vegetative communities. Deer can cause cascading trophic level effects that reduce the biodiversity of the forest (Bressette et al. 2012), and deer at higher densities along the Lake Superior shorelines are already having a measurable negative effect on old growth forest ecosystems (White 2012). Management decisions regarding deer in northeast Minnesota should take into consideration the changes in space use and resource selection between migratory and non-migratory deer in this partially migratory population, and the potential impacts a less migratory population may have on the vegetative community. Investigation into the potential decline of migratory deer and the reasons for the decline should also be undertaken.

Table 2.1. List of independent variables used to develop resource selection function (RSF) models for white-tailed deer in northeast Minnesota at the scale of the home range and the multiple scales of selection. Land cover types within the study area, and associated descriptions, are from the National Land Cover Database (NLCD 2011, Homer et al. 2015). Forest structural variables are Light Detection and Ranging (LiDAR)-derived metrics.

Predictor Variable	Proportion of Study Area	Description
Deciduous	0.20	>20% total vegetation cover and >75% of trees shed foliage simultaneously because of seasonal change
Mixed Forest	0.16	>20% total vegetation cover and neither deciduous or conifer are >75% of canopy cover
Shrub	0.14	>20% total vegetation cover and includes true shrubs and young trees
Conifer	0.16	>20% total vegetation cover and >75% of tree species maintain leaves all year so that the canopy always maintains green foliage
Woody Wetlands	0.22	>20% of vegetation cover is either forest or shrub and soil is periodically covered in water or saturated
Other	0.05	Remaining cover types that, individually, comprise < 10% of the landscape; includes developed cover types, agriculture, and emergent wetlands
Canopy height		Height 75th percentile
Canopy cover		Percent of vegetation returns > 3 m
Understory density		Percent of vegetation returns 1 - 3 m

Table 2.2. Akaike's Information Criterion (AIC) values for deer resource selection function models used in model selection during winter and summer, and for migratory and non-migratory deer within each season. Model variables were land cover (cover), canopy height (h75), canopy density (st1), understory density (st2). K is the number of model parameters, $\Delta AIC = AIC_i - AIC_{min}$, and $w = \exp(-0.5 * \Delta AIC) / \sum \exp(-0.5 * \Delta AIC)$.

Variables	K	AIC	ΔAIC	*w*
		Winter, Migratory		
cover, h75, st1, st2	4	36872	0	0.62
cover, st1, st2	3	36873	1	0.37
cover, st1	2	36881	9	0.01
cover, h75, st1	3	36883	11	0.00
cover, h75, st2	3	36924	52	0.00
cover, h75	2	36937	65	0.00
cover, st2	2	36950	78	0.00
Cover	1	36952	80	0.00
st1, st2	2	37193	321	0.00
h75, st1, st2	3	37195	323	0.00
h75, st1	2	37199	327	0.00
st1	1	37199	327	0.00
h75, st2	2	37265	393	0.00
h75	1	37273	401	0.00
st2	1	37297	425	0.00
		Winter, Non-Migratory		
cover, h75, st1, st2	4	42352	0	1.00
cover, st1, st2	3	42366	14	0.00
cover, h75, st1	3	42376	24	0.00
cover, st2	2	42381	29	0.00
cover, h75, st2	3	42382	30	0.00
cover, h75	2	42408	56	0.00
cover, st1	2	42409	57	0.00
Cover	1	42416	64	0.00
h75, st1, st2	3	42420	68	0.00
st1, st2	2	42430	78	0.00
h75, st1	2	42442	90	0.00
st2	1	42452	100	0.00
h75, st2	2	42454	102	0.00
st1	1	42469	117	0.00
h75	1	42479	127	0.00
		Summer, Migratory		
cover, h75, st1, st2	4	20725	0	1.00
h75, st1, st2	3	21158	433	0.00
cover, h75, st1	3	23055	2330	0.00
h75, st1	2	23552	2827	0.00
cover, h75, st2	3	26019	5294	0.00
h75, st2	2	28696	7971	0.00
cover, h75	2	29310	8585	0.00
h75	1	32184	11459	0.00
cover, st1, st2	3	58310	37585	0.00
cover, st1	2	58360	37635	0.00
cover, st2	2	58371	37646	0.00
Cover	1	58449	37724	0.00
st1, st2	2	59844	39119	0.00
st1	1	59874	39149	0.00
st2	1	59919	39194	0.00

Variables	K	AIC	ΔAIC	*w*
		Summer, Non-Migratory		
cover, h75, st1, st2	4	42082	0	1.00
h75, st1, st2	3	42803	721	0.00
cover, h75, st1	3	44118	2036	0.00
h75, st1	2	44717	2635	0.00
cover, h75, st2	3	57138	15056	0.00
cover, h75	2	59858	17776	0.00
h75, st2	2	61947	19865	0.00
h75	1	64597	22515	0.00
cover, st1, st2	3	117652	75570	0.00
cover, st1	2	117666	75584	0.00
cover, st2	2	117902	75820	0.00
cover	1	117905	75823	0.00
st1, st2	2	118586	76504	0.00
st1	1	118625	76543	0.00
st2	1	119145	77063	0.00

Table 2.3. Mean seasonal distances and start dates of spring and fall migration of deer in 2014 and 2015. Migration start dates were identified using change point analysis and net squared displacement (NSD). Total migration distance was measured as the distance between boundaries of seasonal 95% kernel home ranges. Additional collaring of deer in winter 2014/2015, as well as mortality and collar failures lead to differences in the proportion of migratory deer observed across seasons.

Season	Location	N	Migrators	Migration Distance (Mean ± SE; km)	Start Date (Range)
Spring 2014	Ely	12	33%	6.60 ± 1.91	4-23-2014 (4-4 – 5-14)
	Isabella	9	56%	7.56 ± 2.40	4-28-2014 (3-13 – 6-6)
Fall 2014	Ely	10	40%	6.88 ± 1.89	11-26-2014 (10-27 – 1-3)
	Isabella	6	50%	6.87 ± 1.86	12-4-2014 (11-8 – 1-30)
Spring 2015	Ely	14	21%	9.50 ± 1.18	4-23-2015 (4-15 – 5-30)
	Isabella	16	38%	6.90 ± 1.29	4-19-2015 (3-31 – 5-17)

Table 2.4. 95% kernel seasonal home range sizes of deer in northeast Minnesota during 2014-2015. An average of 1,180 (± 117) locations was used to calculate winter home ranges, and an average of 1825 (± 84) locations was used to calculate summer home ranges.

Season	N	Area ± SE (km^2)	Minimum	Maximum
Winter 2014	9	1.05 ± 0.11	0.57	1.99
Summer 2014	17	1.73 ± 0.43	0.11	5.73
Winter 2015	23	2.22 ± 0.58	0.71	12.61
Summer 2015	24	1.94 ± 0.53	0.07	10.58

Table 2.5. 95% kernel seasonal home range sizes of migratory and non-migratory deer in northeast Minnesota based on GPS locations collected between 2013-2015. Summer was generally from May to late-November, and winter was generally from December to mid-May. Migratory deer had significantly larger home ranges than non-migratory deer in the summer, but not in the winter.

Season	Migratory Strategy	Area ± SE (km^2)
Winter	Non-Migratory	2.01 ± 0.95
	Migratory	1.35 ± 0.48
Summer	Non-Migratory	0.98 ± 0.14
	Migratory	2.09 ± 0.42

Table 2.6. K-fold cross validation results obtained from a 5-fold validation (Boyce et al. 2002, Weins et al. 2008) for top models for migratory and non-migratory deer in each season.

Model	$\overline{r_s}$	P-value
Summer (migratory)	0.98	<0.001
Summer (nonmigratory)	0.99	<0.001
Winter (migratory)	0.70	0.006
Winter (nonmigratory)	0.60	0.01

Table 2.7. Results of mixed-effects logistic regression models of resource selection by migratory and non-migratory deer during winter and summer. Coefficient values are expressed as log odds. The woody wetlands cover type was used as the reference category for the land cover variable.

	Winter		Summer	
	Migratory (β ± SE)	Non-Migratory (β ± SE)	Migratory (β ± SE)	Non-Migratory (β ± SE)
Cover Type				
Conifer	0.16 ± 0.11	0.13 ± 0.09	0.70 ± 0.08	0.20 ± 0.06
Deciduous	0.55 ± 0.11	0.40 ± 0.09	0.90 ± 0.07	0.61 ± 0.05
Mixed Forest	0.43 ± 0.09	0.30 ± 0.09	0.97 ± 0.07	0.40 ± 0.06
Other	-0.38 ± 0.17	0.04 ± 0.14	0.69 ± 0.13	0.67 ± 0.07
Shrub	0.40 ± 0.11	0.32 ± 0.08	1.35 ± 0.10	0.61 ± 0.05
Canopy Height	0.002 ± 0.05	-0.06 ± 0.04	0.14 ± 0.07	-0.01 ± 0.03
Canopy Cover	0.13 ± 0.04	0.13 ± 0.04	-0.12 ± 0.03	-0.12 ± 0.02
Understory Density	0.11 ± 0.03	0.07 ± 0.04	0.11 ± 0.03	-0.03 ± 0.02

Table 2.8. The average proportion of each cover type (+/- SEM) used and available to deer within 95% kernel home ranges during summer and winter in 2014 and 2015.

	Summer				Winter			
	2014		2015		2014		2015	
Cover Type	Used	Available	Used	Available	Used	Available	Used	Available
Conifer	15 (6)	17 (5)	17 (6)	20 (5)	33 (10)	31 (7)	18 (5)	19 (4)
Deciduous	28 (12)	25 (11)	23 (8)	17 (6)	7 (2)	6 (1)	20 (7)	14 (3)
Mixed Forest	25 (6)	23 (5)	17 (4)	15 (3)	26 (7)	21 (6)	21 (6)	20 (4)
Other	7 (3)	6 (1)	8 (4)	6 (1)	3 (1)	5 (2)	6 (4)	6 (2)
Shrub	15 (6)	13 (5)	24 (6)	17 (4)	17 (6)	14 (5)	15 (5)	15 (4)
Woody Wetlands	16 (5)	21 (4)	13 (4)	25 (6)	17 (8)	24 (7)	21 (7)	24 (6)

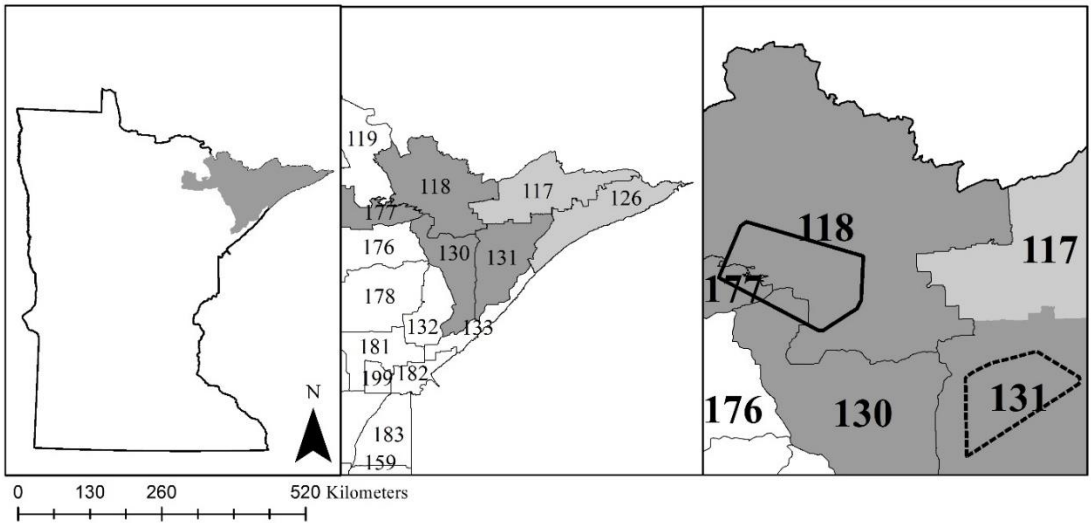


Figure 2.1. Study areas in northeast Minnesota (1,530 km^2 total). Deer permit areas are highlighted in gray. The polygon outlined in solid black is the Ely study area and the dotted polygon is the Isabella study area.

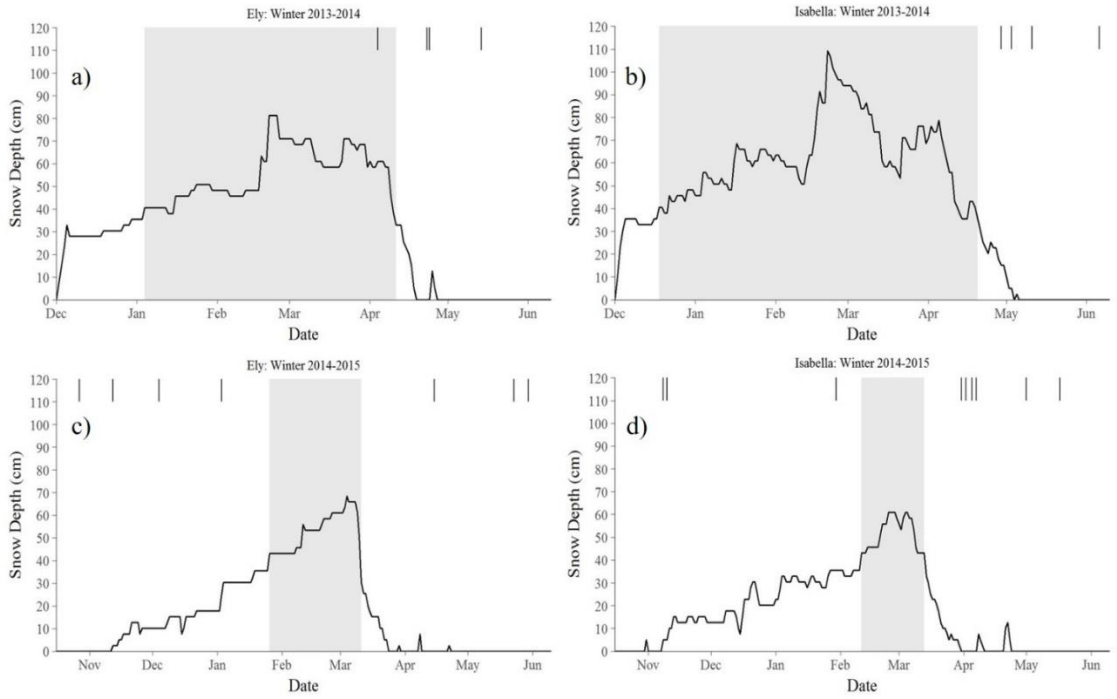


Figure 2.2. Fall and spring migration dates relative to snow depth at each study site in each year of the study. Solid black lines represent snow depth on the y-axis and dates are given on the x-axis. Gray shading indicates the period when snow depth exceeded 38-cm each year. Dashed black lines at the top of each panel indicate migration dates for each migratory deer. Only one migration took place when snow depth was greater than the 38-cm threshold.

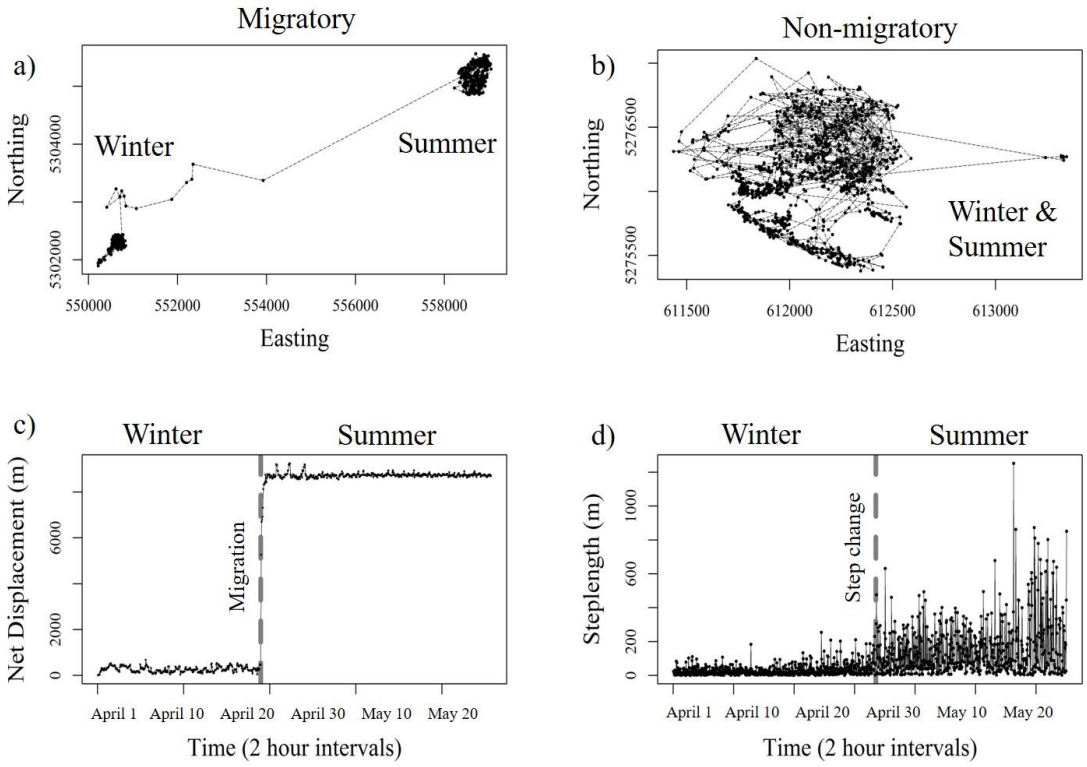


Figure 2.3. Examples of locations and paths of a migratory (a) and non-migratory (b) deer with associated net displacement figures segmenting winter from summer using changepoint analysis to identify migration from winter to summer range (c) and change in step length for non-migratory deer (d). The movement pattern displayed in panel d is also observed in migratory deer as step length changes with migration, however; change in step length does not provide information about migratory status and so could not be used to differentiate between migratory and non-migratory deer.

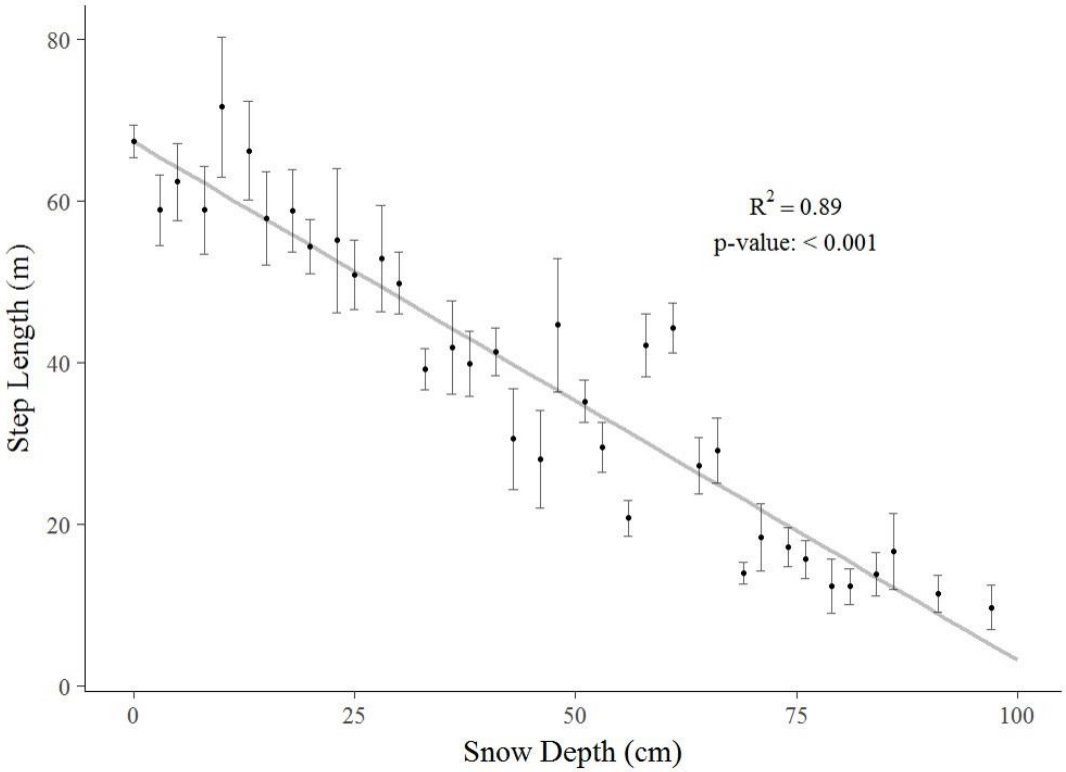


Figure 2.4. Linear regression of average step length as a function of snow depth. Points are average step lengths at each snow depth measurement. Error bars are 95% confidence intervals. Step length was calculated as the linear distance between consecutive locations obtained at 2-hour intervals. Snow data was collected daily at NOAA RAWS sites in Ely and Isabella, MN.

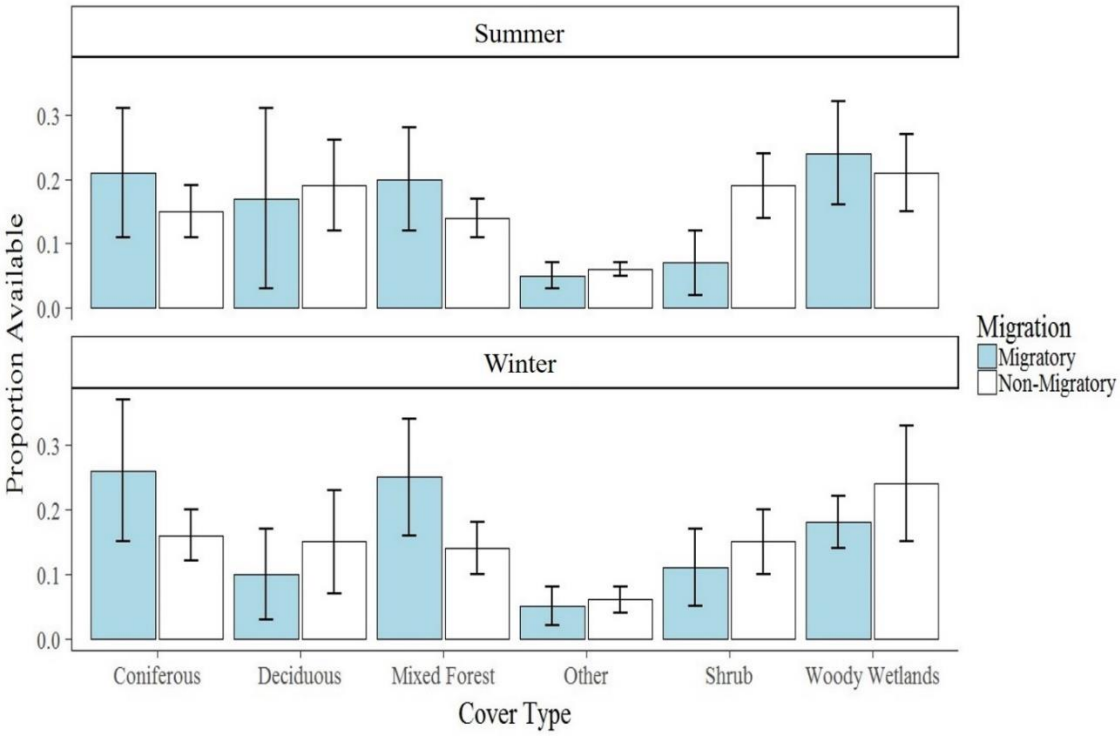


Figure 2.5. Proportion of land cover types available within summer home ranges and winter home ranges of migratory deer (light blue) and non-migratory deer (white). The error bars are 95% confidence limits.

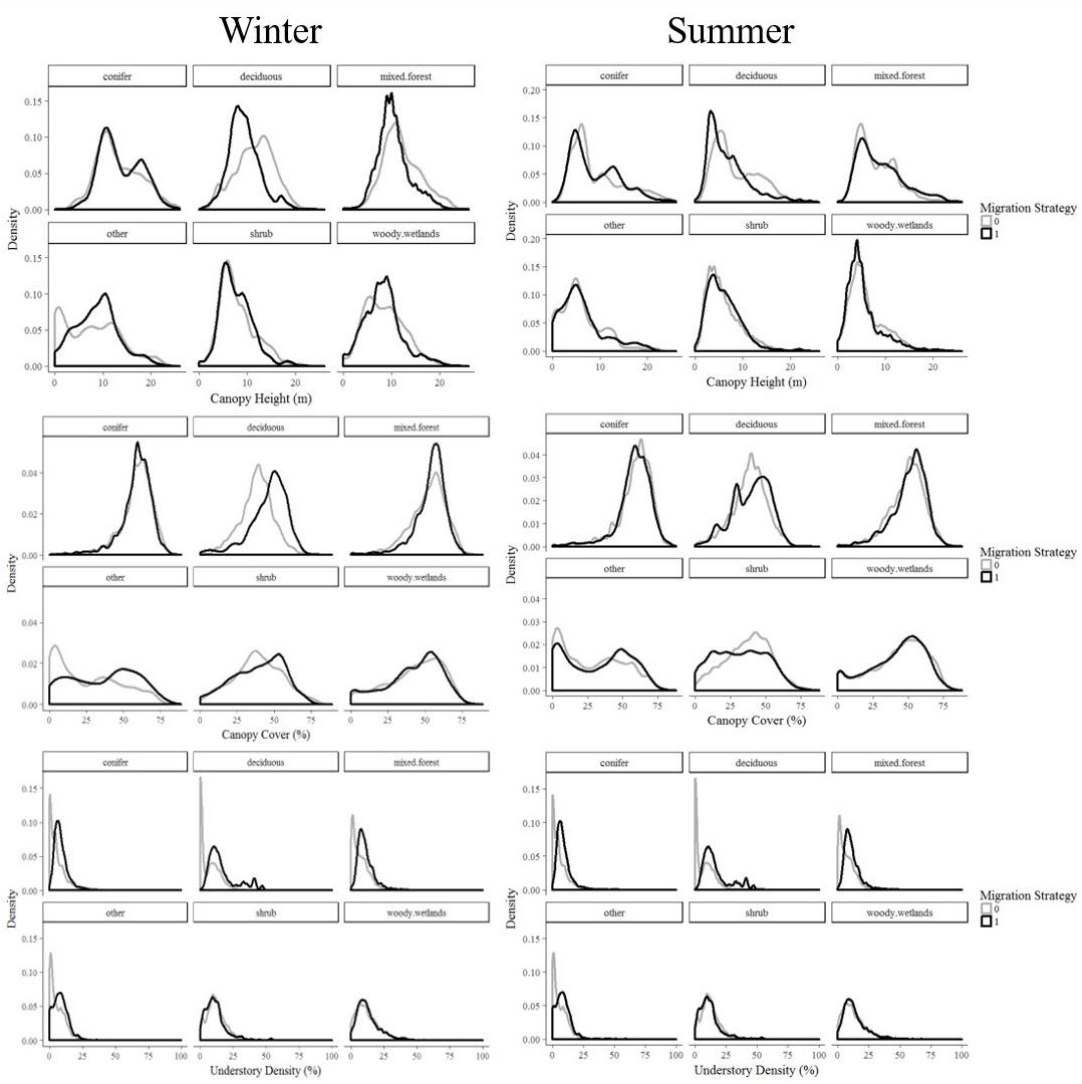


Figure 2.6. Distribution of forest structural components for non-migratory deer (gray lines) and migratory deer (black lines) in the snow season and the non-snow season. Distributions were generally similar between season and migratory strategy.

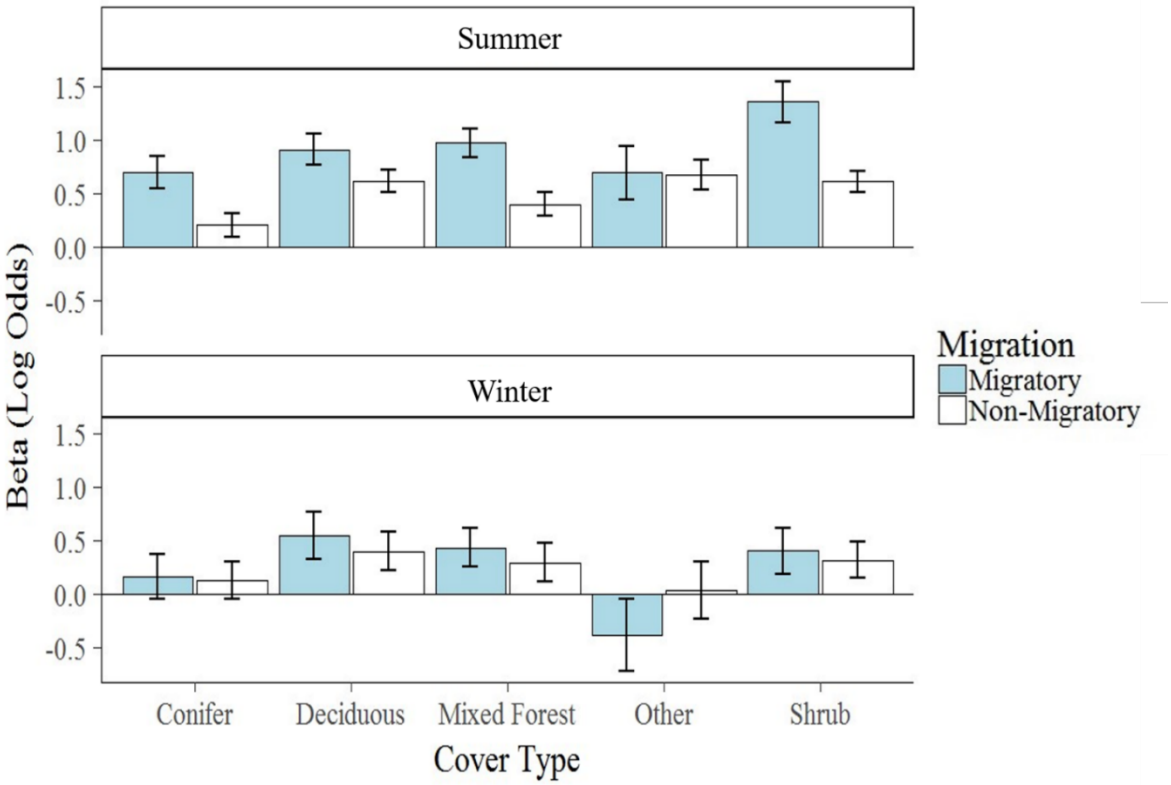


Figure 2.7. Coefficient values with 95% confidence error bars for deer land cover selection in snow and non-snow seasons. Selection is relative to the woody wetlands land cover type. Blue bars are migratory deer and white bars are non-migratory deer. Coefficients are log odds and considered significant if confidence limits did not include zero.

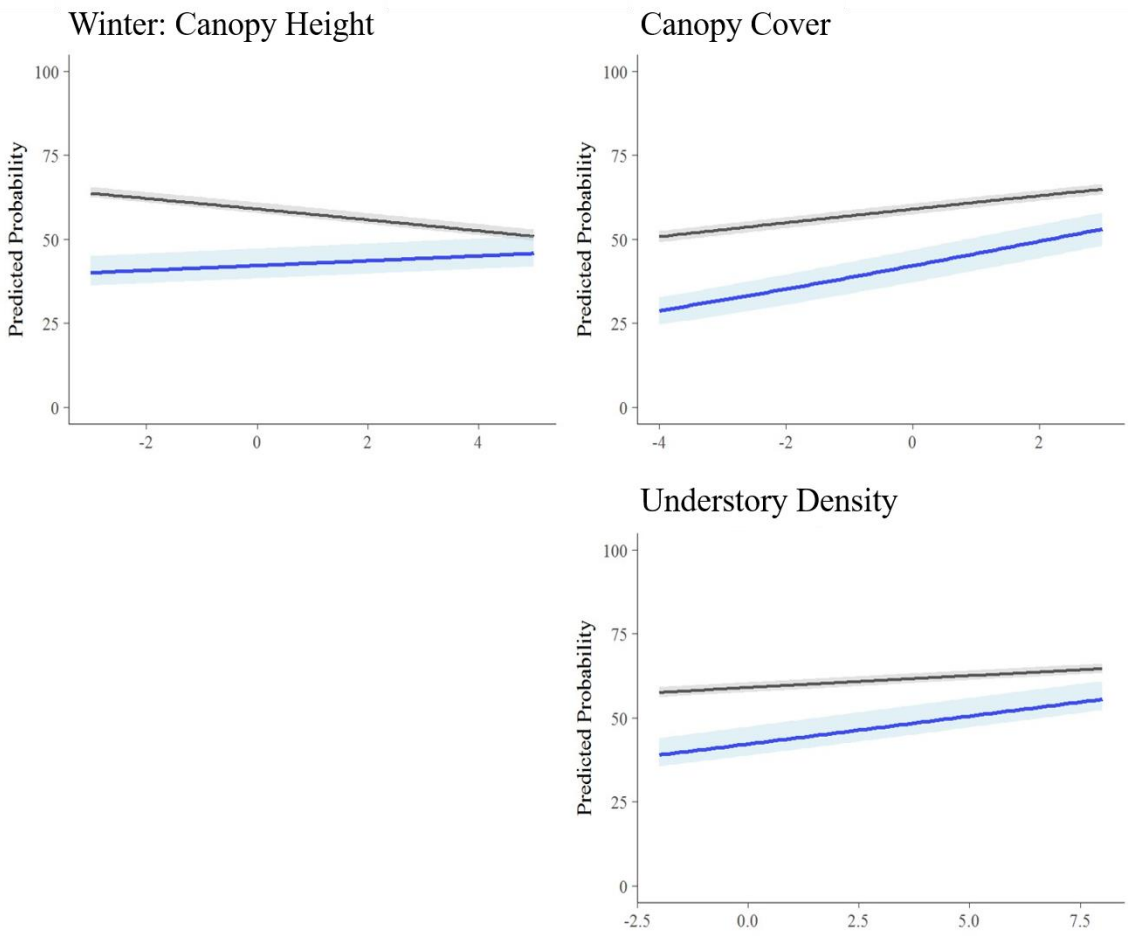


Figure 2.8. Relative probability of selection for forest structural components by migratory deer (blue line) and non-migratory deer (black line) in the winter. The x-axis is the scaled value for canopy height, canopy cover, and understory density. Ribbons represent 95% confidence interval for relative probability of selection by migratory deer.

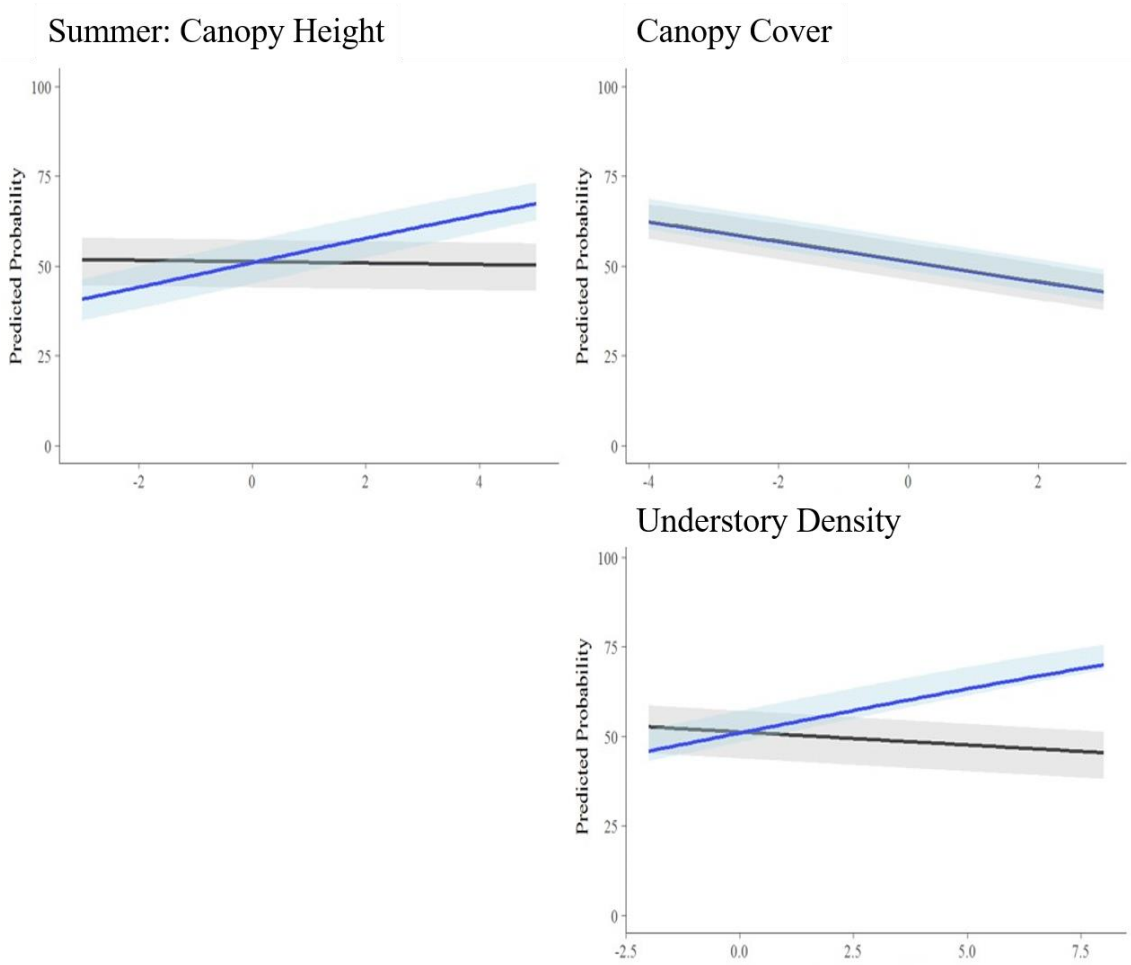


Figure 2.9. Relative probability of selection for forest structural components by migratory deer (blue line) and non-migratory deer (black line) during the summer. The x-axis is the scaled value for canopy height, canopy cover, and understory density. Ribbons represent the 95% confidence interval for relative probability of selection by migratory deer. There is overlap in the lines for migratory and non-migratory deer relative probability of selection for canopy cover.

Chapter 3
Resource selection by moose in northeast Minnesota

Preface

Large herbivore habitat use is dependent on need of a resource by the animal and availability of the resource, which is influenced by the suite of environmental attributes of an area and which changes over time. Understanding how resource use is influenced by season and time of day will improve our ability to adaptively manage large herbivores. We tracked 30 moose (*Alces alces*) using global positioning system (GPS) radio collars in northeast Minnesota from 2011-2012. We partitioned data into spring, summer, fall, and winter, behavior within seasons, and day or night within seasons to test for patterns of resource selection at various temporal and behavioral scales. Fine-scale forest structural data was available from Light Detection and Ranging (LiDAR) derived metrics and were included along with coarse-scale cover type data in resource selection models. Moose resource selection patterns for cover type were strongest at the seasonal scale and generally followed phenological patterns of forage availability. Woody wetlands was used as the reference cover type in resource selection models. Moose selected for all forested cover types that provide food and shelter in winter, spring, and summer, but avoided all forested cover types in the fall when the remaining green forage can be found predominantly in woody wetlands. Within seasons, at behavioral and day/night scales, selection patterns for fine-scale forest structural components indicated that moose could take advantage of micro-habitats within coarser land cover types to meet forage and thermal cover requirements. The variability in selection patterns was most pronounced in spring and fall, and we suggest that these time periods not be overlooked in moose habitat management plans.

Key words: *Alces alces*, habitat, Minnesota, moose, resource selection

Introduction

Moose daily time budgets are polyphasic with 95% of their day spent alternating between periods of activity when moose search for and acquire forage, and periods of inactivity when moose rest or ruminate (Risenhoover 1986, Cederlund 1989, Van Ballenberghe and Miquelle 1990). Other activities such as walking, running, and grooming account for <5% of a moose's daily time budget (Van Ballenberghe and Miquelle 1990). The proportion of time spent either resting and ruminating or foraging each day is influenced by seasonal changes in forage quantity and quality, as well as seasonal and daily variation in weather (Cederlund 1989).

In addition to behavioral adjustments to accommodate seasonal variation in forage quantity and quality, moose also express metabolic plasticity (Regelin et al. 1985, Schwartz et al. 1987). Moose metabolism slows in winter as their diet shifts to woody twigs and conifer needles which are less digestible than green leafy material ingested during summer. Changes in forage availability and quality, along with changes in metabolism (Regelin et al. 1985, Moen et al. 1997, Schwartz et al. 1987) result in longer periods of resting and ruminating and shorter periods of activity in winter compared to summer (Risenhoover 1986).

Because moose spend most of their daily time budget either foraging, resting, or ruminating, the availability and distribution of food and shelter in time and space should have a strong influence on behavior patterns and resource selection (Cederlund 1989). Accurately estimating time allotted to foraging and resting behaviors is essential to understanding patterns of resource selection across spatio-temporal scales. Identifying specific behaviors requires determining the scale at which the animal is operating.

Behaviors such as foraging are often restricted to patches of the same cover type for individual bouts and decisions are made at the plant community scale (Senft et al. 1987, Johnson et al. 2002), whereas travel between distinct large foraging patches is inter-patch and is influenced by spatial heterogeneity at the landscape scale (Johnson et al. 2002).

Using biologically-based criteria to define seasons and behaviors with data from global positioning system (GPS) collared moose will allow us to estimate the seasonal and behavior-specific importance of various resources and will improve our understanding of moose ecology throughout the year. Knowing which habitat components are selected by moose over the course of a year at a fine temporal scale and being able to assign behaviors to each location would be a powerful tool for determining important resources (e.g. foraging habitat) and how selection changes across spatio-temporal scales. However, few studies have scaled behavioral data up to provide information on habitat use at the landscape level because of sample size requirements and the high costs associated with the technology needed to make population level inferences (Owen-Smith et al. 2010).

Our objectives were to determine whether there were differences in resource selection patterns by free-ranging moose among seasons, between night and day, and when active or inactive within seasons. We expect to observe variance in resource selection at a seasonal scale. We also hypothesize that patterns of resource selection will be different between day and night, and that variation in daily selection may be driven by physiological needs related to thermoregulation, with moose selecting for forest cover types and structural components that provide thermal cover during the day when temperatures are highest, while selecting open cover types and forest structural

components that allow for radiant heat loss at night when temperatures are lowest. Our behavior-specific hypotheses are that moose will be inactive in areas more likely to allow for thermoregulation during the day when temperatures are highest, and that moose will be active in areas more likely to have abundant forage available.

Study Area

We conducted this study in northeast Minnesota, USA (Figure 3.1). The Isabella study site (centered on latitude: 47° 30' N, Longitude: 91° 20' W) was 2804-km^2 and the Grand Marais study site (centered on latitude: 47° 52' N, Longitude: 90° 14' W) was 330-km^2. Public lands managed for timber harvest and recreation constitute >80% of property ownership, most of it being federal land interspersed with smaller parcels of state, county, and tribal holdings. Primary predators of moose in the region are wolves (*Canis lupus*) and American black bears (*Ursus americanus*). The study area is in the Laurentian Mixed Forest, which transitions from northern hardwood forests in the south to boreal forests in the north (Pastor and Mladenoff 1992). Fire-dependent upland forests are a mixture of white pine (*Pinus strobus*), red pine (*P. resinosa*), jack pine (*P. banksiana*), aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*). Conifer swamps of tamarack (*Larix laricina*) and black spruce (*Picea mariana*) dominate the lowlands (Minnesota Ecological Classification System 2008). The climate is continental with moderate to severe winters and warm summers. July is the warmest month and the average high temperature from 2002-2012 was 19° C (National Oceanic and Atmospheric Administration [NOAA] 2012). January is the coldest month and the average low temperature from 2002 to 2012 was -13° C (NOAA 2012). Snow

cover is typically present from December to April, with annual snowfall regularly reaching 180-cm**.**

Methods

Animal capture and GPS collaring

We captured moose by darting them from helicopters during January and February 2011. Moose were chemically immobilized using 1.2 ml (4.0 mg ml^{-1}) carfentanil citrate and 1.2 ml (100 mg ml^{-1}) xylazine HCl. We used 7.2 ml (50 mg ml^{-1}) naltrexone HCl and 3 ml (5 mg ml^{-1}) yohimbine HCl as the antagonist (see McCann et al. 2016 for additional capture details). We collected blood, hair, and feces from each moose. Morphological measurements taken included chest girth, neck circumference, and total body length. Immobilized moose were also fitted with GPS collars (Lotek Wireless, Inc., Newmarket, Ontario, Canada). GPS radio collars recorded locations every 20-minutes with an expected battery life of two years (Lotek Wireless, Newmarket, ON, Canada). Collars were also equipped with activity loggers that recorded activity every five minutes for two years. Collars contained drop-off mechanisms programmed to release collars two years after deployment. Animal capture and handling protocols met the American Society of Mammalogists recommended guidelines (Sikes et al. 2011) and were approved by the University of Minnesota Animal Care and Use committee (Protocol Number**:** 1309-30915A).

We retained GPS locations with 3-D fixes or 2-D fixes with dilution of precision values ≤5 (Lewis et al. 2007, Bjørneraas et al. 2010), and excluded locations that were not biologically possible (i.e. locations where the movement rate from the last location

would have exceeded the distance a moose could have moved in a 20-minute period, assuming a maximum speed of 55-km/hour ("Minnesota Mammals – Moose" MN DNR 2018). Moose were excluded from seasonal analyses if there was < 30-days of location data available within a season. This occurred either when a moose died or when a GPS collar failed. Location and activity data within 14 days of capture were censored from the final datasets to reduce potential biases in movement and habitat use related to recovery from capture.

Habitat variables metadata

We characterized moose habitat by lumping the two study sites within the larger study area, and by using different sources of remotely sensed data: coarse landcover data from the National Land Cover Database (NLCD) and Light Detection and Ranging (LiDAR) derived metrics of forest structural components (Table 3.1). Land cover types were determined using the 2011 National Land Cover Database (Homer et al. 2015). The NLCD is a dataset of land cover created from Landsat Thematic Mapper imagery every five years with 30-m spatial resolution (Homer et al. 2015). Sixteen land cover types are defined in the NLCD dataset. Forest, shrub (12%), and woody wetlands (39%) cover types were separate cover types in the models (Table 3.1). Forest cover types included deciduous forest (14%), coniferous forest (16%), and mixed forest (16%). We classified cover types making up < 5% of the landscape as 'other'. The 'other' land cover category comprised 4% of the landscape and included human developments, agriculture, grasslands, and emergent aquatic wetlands.

We used LiDAR data to characterize forest structural heterogeneity within coarse land cover classes. In May 2011, LiDAR data was collected over the entire study area

during leaf-off conditions (MN Geospatial Information Office, 2015). The LiDAR-derived metrics of habitat structural heterogeneity were averaged over each 30-m pixel within the study area. Forest canopy height was estimated using the 75th percentile of LiDAR-derived canopy height measurements to avoid undue influence from super-canopy white pine that occur within mixed forests and coniferous forests in the region. The canopy cover measure was estimated from the proportion of non-ground returns above 3-m from ground level. The understory density index was estimated from the proportion of non-ground returns above 1-m and below 3-m.

Season classification

We defined biologically meaningful seasons for moose based on behavioral patterns and weather patterns (Table 3.2). Snow and ambient temperature data were obtained from the Isabella, Minnesota NOAA RAWS Climate Archive (RAWS USA Climate Archive, 2016), which reports daily minimum, maximum, and average temperatures, and daily snow or rain precipitation and accumulation. For our purposes, winter was when there was snow on the ground, which was typically from early January (when captures occurred) to April 23, 2011 in the first year of the study and November 26, 2011 to March 16, 2012 in the second year of the study. Spring started with the loss of snow cover (April 24 in 2011 and March 17 in 2012) and ended at parturition. The average parturition date in Minnesota is May 15. Parturition can be accurately determined for moose based on a distinct behavior pattern where female moose move long distances to a parturition site where they then localize for one to two weeks (McGraw et al. 2014). The end of spring was thus defined for each female moose as the point in time before the start of the long-distance movement to the parturition area. Male moose, on the other

hand, do not make long-distance spring movements. We used the average of the female long-distance movement dates to define the end of spring for male moose. Because we considered the parturition date to be the end of spring, the entire green-up time period was likely not included and so the diet transition from twigs to leaves was not fully covered. We excluded the period when moose localized after parturition (McGraw et al. 2014) and defined the start of summer as 21 days past the average of the long-distance parturition movement date for several reasons. First, female moose significantly restrict movements and remain in patches of about 1.75-ha during the post-parturition period (McGraw et al. 2014). Second, active bouts during the post-parturition period would be either care-giving to calves or foraging. The end of summer was defined as the day before the first frost was likely, based on temperature and frost tables for the region. The beginning of fall was the first day after summer ended (September 6 in 2011 and September 16 in 2012) and lasted until the first snow fall resulting in snow accumulation, based on the criteria defined above for the start of winter. Fall thus encompassed the loss of green foliage and a transition in moose diet from leaves to twigs. Once seasons were defined, we classified GPS locations into the appropriate season. We also classified each moose location into day or night based on the GPS location timestamp and sunrise and sunset times for Isabella, Minnesota.

Partitioning movement patterns

Internal GPS collar activity loggers were dual-axial and polled x- and y-axes four times/second. Records were summed, and a value was produced at the end of every 296-seconds after a correction factor was applied using an internal algorithm. The algorithm was not provided by the collar manufacturer. Values ranged from 0-255 on each axis for

each five-minute period. Activity data were stored on-board and were available only if the collar was recovered at the end of the study.

To determine when moose were active or inactive, homogeneous segments of x-axis activity values for each day were identified using the PELT (Pruned Exact Linear Time) changepoint detection algorithm (Killick and Eckley 2012 & 2013; Package: changepoint, R. Killick and Eckley, 2014). We only used x-axis data from activity loggers because the x-axis counts and y-axis counts were highly correlated (McGraw, *unpublished data*). The PELT algorithm recursively iterated through the activity logger data for each individual and across the entire time series and identified breakpoints in segments where significant deviances in mean and variance in activity existed (significance levels: $\alpha < 0.05$, Madon and Hingrat 2014). Using this approach, the locations of change points represented the start and end points of active and inactive bouts. We visually inspected changepoint locations to determine whether the algorithm was working well, and adjusted parameter values in the algorithm until changepoints matched our visual interpretations of behavioral changes. We then calculated the average activity value of each homogeneous segment.

To assign segments to active or inactive behaviors, we used threshold activity values that were determined by visual observations of collared moose in Alaska (Herberg, 2017). Average segment values above the threshold indicated that moose were active, while average segment values under the threshold indicated when moose were inactive. We used the upper bound of the 95% confidence interval for observed inactive behaviors of collared moose in Alaska (Herberg 2017) as the threshold value to assign segments identified by changepoint analysis of activity logger data to active or inactive

behaviors. In winter, segments with mean activity values <5 were categorized as inactive, whereas segments with mean activity values ≥ 5 were categorized as active. During spring, summer, and fall, activity segments with mean values ≥ 25 were classified as active. We tested for differences in the length of bouts of activity or inactivity between seasons using Analysis of Variance (ANOVA) and post-hoc Tukey tests.

Resource selection

To evaluate patterns of resource selection by moose at seasonal and day/night temporal scales, and when moose were active and inactive, we used resource selection functions (RSFs) following a type III design, where available resource units are measured at the individual level within a home range (Manly et al. 2002). For each used point within winter and summer home ranges we created one random point to represent available resources within home range boundaries (Manly et al. 2002, Laforge et al. 2015). Locations for winter were used to delineate winter home ranges while spring, summer, and fall locations were used to delineate composite home ranges that we called summer home ranges. Each home range was constructed by calculating 95% bivariate normal kernels using the reference bandwidth (Package adehabitatHR, Program R; Calenge 2006), using 20-minute locations for each moose. One moose migrated between winter and spring/summer/fall ranges in the study. The migration route locations were removed before the calculation of seasonal home ranges and the data from that moose was retained in the study. We tested for variation of home range sizes by season, year, and sex using ANOVA tests and post-hoc Tukey tests.

Each GPS location was assigned to an active behavior or inactive behavior category where timestamps of the activity logger value and the GPS location matched. Each

random point was randomly assigned a behavioral state (active or inactive) and a day or night value. We tested for differences in activity levels and behavioral bout lengths between male and female moose in all seasons using ANOVA.

Seasonal, day vs. night, and behavior-specific RSFs were estimated using logistic generalized linear mixed models using the 'glmer' function in the lme4 package (Bates et al. 2015) in R (R Core Team 2016):

(1) $w(x) = \exp(\beta_{1ij}x_{1ij} + \cdots + \beta_{nij}x_{nij} + \gamma_{0j})$

where $w(x)$ is the relative probability of use, B_i are the log odds coefficient values, x_{1ij} are the coefficients, and γ_{0j} is the random intercept for individual animals (*n* designates the covariate, *i* designates the observation, and *j* designates the group (Gillies et al. 2006)).

Unequal sampling and individual variability was controlled for by including individual animals as a random effect in each model. Data were rarified to 20% of the full dataset by selecting every 5th data point for each animal. Continuous covariates were *z*-transformed. The woody wetlands cover type was used as the reference category in all models because it constitutes a large portion of the landscape and because one habitat type in the categorical land cover variable must be removed for dummy variable coding (Boyce et al. 2002). Covariates included in the candidate model sets included land cover as a categorical variable, and canopy height, canopy cover, and understory cover as continuous variables.

The top model was selected from a set of *a priori* candidate models (Burnham and Anderson 2002, Table 3.3) for each behavioral and day/night model set, during each season, based on Akaike's Information Criteria (AIC). We performed a 5-fold k-fold

cross validation with Spearman rank correlation to determine the goodness-of-fit of the top model identified by AIC (Boyce et al. 2002, Weins et al. 2008). Regression coefficients were considered significant if 95% confidence intervals, calculated from the model coefficients and standard error estimates, did not overlap zero. We calculated the correlation coefficient values for coefficient values between seasonal models and behavior-specific models within a season, and between seasonal models and day/night models within a season.

Results

We captured 21 adult female (>2-years), eight adult male (>2-years), and one yearling male (<2-years) moose. Location data were available for all moose; however, activity data were available only for a subset of collared moose (n=18) because drop-off mechanisms failed, and collars were not recovered for three moose. If collars were not recovered, stored activity data could not be used in behavior analysis. As a result, we were able to conduct behavior-specific resource selection probability function analysis for 19 moose in the summer and 18 moose during the winter, only three of which were male. During winter the average number of GPS locations used in RSF models was 5,672 (SE ± 289) and the average number of GPS locations was 1,869 (SE ± 225) in the spring, 6,152 (SE ± 161) in the summer, and 4,251 (SE ± 269) in the fall.

We calculated seasonal home ranges for 21 female and eight male moose from GPS locations (Table 3.3). Separate seasonal home ranges were made for each moose if collar data was available for more than one year (i.e. there were two summer home ranges calculated for a moose collared for two years). Males had larger home ranges than females in winter (50.2-km^2 ± 29.8-km^2 and 24.9-km^2 ± 7.6-km^2, respectively), and in

summer (65.67-km^2 ± 15.6-km^2 and 23.3-km^2 ± 3.5-km^2, respectively, $F_{3,64} = 3.037$, $p = 0.03$).

The availability of cover types was similar for moose on winter and summer home ranges, and cover types available within seasonal home ranges were similar to the overall availability of cover types throughout the study area (Figure 3.2). The woody wetlands cover type was the most prevalent cover type in both summer and winter home ranges (33% ± 3% and 36% ± 4%, respectively), as well as the most prevalent cover type in the study area. The other major cover types were available in similar proportions to each other, with summer home ranges consisting of 15% ± 1% conifer, 16% ± 3% deciduous, 18% ± 2% mixed forest, and 13% ± 2% shrub stands. Winter home ranges consisted of 15% ± 2% conifer, 13% ± 2% deciduous, 18% ± 2% mixed forest, and 14% ± 2% shrub stands. The distribution of forest structural components within cover types did not appear to differ significantly between cover types, with similar patterns of canopy height, canopy cover, and understory density (Figure 3.3).

Bouts of activity and inactivity were shortest in summer (length of active bout: 69-min ± 0.5-min, length of inactive bout: 104-min ± 0.6-min). Bouts of inactivity were longest in winter and spring (Table 3.4). The length of active bouts in spring was more than double the length of active bouts in any other season (250-min ± 11-min). Active and inactive bouts in the fall were intermediate in length compared to summer and winter (active: 76-min ± 1-min; inactive: 130-min ± 1.5-min). Minor peaks in active behavior throughout the day occurred around sunrise and sunset (Figure 3.4).

Seasonal resource selection by moose

The best model of resource selection for moose was the same across seasons, night/day within seasons, and behavior within seasons, and contained cover type, canopy height, canopy cover, and understory density as covariates (Table 3.5 and Table 3.6). Cross-validation scores for resource selection indicate the model was robust at the season scale, and at day and night and behavioral scales within seasons ($r_s \geq 0.93$, Table 3.9). The woody wetlands cover type was the reference category for cover type in each model, and so descriptions of cover type selection are all relative to the woody wetlands cover type.

The correlation among coefficient values between seasonal models and night and day models, and between seasonal models and behavior models was high in winter and spring, indicating that habitat selection was similar regardless of whether it was night or day, or if moose were active or inactive (Table 3.8). Correlation among seasonal models and within-seasonal day/night and behavioral models was lowest during the summer and fall (Table 3.8).

During the winter, moose selected deciduous forests, conifer forests, mixed forests, and shrub stands, relative to woody wetlands. Moose avoided the 'other' cover type in winter (Table 3.6, Figure 3.5). Moose cover type selection patterns in winter did not change relative to whether moose were active or inactive (Figure 3.6) or relative to whether it was day or night (Figure 3.7). Dense understories were selected in winter while tall canopies and high canopy cover were avoided, again regardless of whether moose were active or inactive or whether it was day or night (Table 3.6, Figure 3.8, Figure 3.9, Figure 3.10).

During the spring moose selected deciduous forests and mixed forests, but avoided conifer forests, shrub stands, and the 'other' cover type, relative to woody wetlands (Table 3.5, Figure 3.5). Like winter, patterns of moose cover type selection were not dependent on whether moose were active or inactive (Figure 3.6), or whether it was day or night (Figure 3.7). Moose also selected taller canopies and denser understories in the spring, but avoided high canopy cover (Table 3.5, Figure 3.8, Figure 3.9, Figure 3.10), regardless of behavior or whether it was day or night.

In summer, moose selected deciduous forests, conifer forests, mixed forests, and shrub stands regardless of whether they were active or inactive (Table 3.5, Figure 3.6), or whether it was night or day (Table 3.5, Figure 3.7). The 'other' cover type was avoided when moose were active and inactive (Figure 3.6), and also during the day, but was used in proportion to availability at night (Table 3.5, Figure 3.7). Tall canopies were avoided regardless of whether moose were active or inactive in summer, and during the day in summer, but were used in proportion to availability at night (Table 3.5, Figure 3.8). High canopy cover was avoided when moose were active and inactive (Table 3.5, Figure 3.9). Canopy cover was also avoided at night during the summer, but was selected during the day (Table 3.5, Figure 3.9). Dense understories were avoided when moose were active and used in proportion to availability during the summer (Table 3.5, Figure 3.10). Dense understories were also selected during the day and avoided at night during summer (Table 3.5, Figure 3.10).

Regardless of whether they were active or inactive (Figure 3.6), or whether it was night or day (Figure 3.7) moose consistently avoided deciduous and coniferous forests in the fall, relative to the woody wetlands cover type. Mixed forests were selected by moose

at night and used in proportion to availability when moose were active but were otherwise avoided in the fall (Table 3.6, Figure 3.5, Figure 3.6). Shrub stands were selected at night and when moose were active but were avoided during the day and when moose were inactive in the fall (Table 3.6, Figure 3.6, Figure 3.7). The 'other' cover type was consistently avoided in the fall (Figure 3.6, Figure 3.7), as were tall canopies (Figure 3.8) and canopy cover (Figure 3.9). Dense canopies were selected by moose during the day and when they were active in the fall but were avoided when moose were inactive and used in proportion to availability at night (Table 3.6, Figure 3.9).

During the summers of 2011 and 2012 deciduous forests, mixed forests, shrub lands, and woody wetlands made up a total of 79% and 83%, respectively, of the habitat available to moose within their summer home ranges whereas those habitat types accounted for 83% and 87% of the habitats used by moose during summers 2011 and 2012, respectively (Table 3.10). Conifer habitat available to moose during summers 2011 and 2012 made up 16% and 14% of their home ranges, respectively while conifer forests accounted for 14% and 10% of habitat use by moose in summers 2011 and 2012, respectively (Table 3.10). To contrast, during the winters of 2011 and 2012, deciduous forests, mixed forests, shrub lands, and woody wetlands made up 79% and 84%, respectively, of the available habitat within moose winter home ranges whereas those habitat types made up 81% and 91% of the habitats used by moose during winters 2011 and 2012, respectively (Table 3.10). Conifer forest availability within winter moose home ranges was 19% and 15% during winters 2011 and 2012, respectively while conifer forest use within winter moose home ranges was 18% and 8% during winters 2011 and 2012, respectively (Table3.10).

Discussion

We found that moose exhibited patterns of resource selection that were apparently influenced by season, whether it was day or night, and whether they were active or inactive. This suggests that moose habitat selection in northeast Minnesota may depend on trade-offs in habitat use as it relates to fluctuations in environmental conditions and resource availability. Previous studies support our inferences that moose habitat selection is a functional response to changing environmental conditions to meet basic life-history needs. For example, Street et al. (2016) also noted changes in patterns of moose habitat selection relative to time of day and ambient temperature, observing an increased use of conifer forests and a decreased use of deciduous forests when temperatures were highest during midday. Street et al. (2016) concluded that during the summer moose in Minnesota primarily selected habitats based on forage availability, and that limited use of deciduous forests because of abiotic environmental conditions such as temperature could negatively impact moose foraging efficiency.

Across seasons, moose in our study selected for deciduous and mixed cover types that likely provide the most forage. The pattern of selection for forage producing areas appeared to follow phenological trends, with moose selecting for deciduous forests that would be among the first cover types to green-up in spring (shrub being the other cover type to green-up early in spring), and then selecting all forage-producing forest types such as deciduous forests, mixed forests, and shrub stands in summer during full leaf-out, while using these cover types less in fall during senescence. This observation is supported by previous studies concluding that ungulate habitat selection within seasonal home ranges is often a trade-off between food and shelter (Rettie and Messier 2000, Johnson et al. 2002, Dussault et al. 2005). For example, upland deciduous forests are often a source

of consistent food resources for moose throughout the year (Courtois et al. 2002), though woody wetlands are typically the last of the cover types to provide green forage in the fall (Timmerman and McNicol 1988). Moose often forage on shrubs such as red osier dogwood (*Cornus sericea*) in the fall, which are associated with woody wetlands (Timmerman and McNicol 1988, Ward 2015). Foraging on remaining green digestible species in woody wetlands after leaf-fall in upland forests in the fall (Timmerman and McNicol 1988) could allow moose to extend the period of weight gain before winter sets in and moose are in negative energy balance.

Thermal cover for moose is often cited as an important habitat component (Demarchi and Bunnell 1995, Dussault et al. 2004, McCann et al. 2013), especially at the southern edge of their range where temperatures can reach levels believed to cause thermal stress in moose (Renecker and Hudson 1986, McCann et al. 2013, Street et al. 2016). We found that selection for cover types that provide thermal shelter followed a seasonal pattern as well, with moose selecting conifer forests in winter and during the summer but using them less in the spring and fall, relative to the woody wetlands cover type. More specifically, moose in our study selected for cover types that potentially provide thermal cover during the day in summer, while avoiding them at night. This is similar to patterns of selection for thermal cover observed in Ontario, Canada, where moose increasingly selected for habitat types that provide thermal cover as a result of high temperatures reached during the day in summer (Street et al. 2015). Similarly, in Quebec, Canada, moose selected mature conifer stands in summer and early winter, and young conifer stands in late winter (Courtois et al. 2002). Moose are sensitive to warm temperatures in winter, and there is some evidence of a negative correlation between

moose survival and winter average high temperatures (Lenarz et al. 2009, Lenarz et al. 2010).

Moose selected for taller, less dense canopies, and denser understories in winter and spring, though selection for denser understories was stronger in spring than in winter. Moose enter spring in the poorest body condition of the year after surviving a winter spent in negative energy balance (Moen 1978). Female moose are also nearing parturition in early spring, and so in addition to a winter spent in negative energy balance, they also need to meet the energetic requirements of gestation and have enough energy reserves for lactation after parturition (Regelin et al. 1985). Therefore, as green-up occurs in spring it is expected that moose would spend more time in areas that provide more forage.

Similar to spring, moose selected less dense canopies in the fall. However, in contrast to spring selection patterns, moose avoided taller canopies and denser understories were not selected by moose in the fall. This could be a function of moose feeding in woody wetlands in the fall, which have shorter, less dense canopies with understories that remain green and provide forage for longer than upland forest types (Timmerman and McNicol 1988).

Variation in selection for fine-scale forest structural components was most pronounced between day and night within seasons. There is evidence that avoidance of dense canopy cover by active moose in the fall meant more time was spent in woody wetlands, which serve the dual purpose of alleviating thermal stress (Street et al. 2016) while providing the last of the year's green forage (Timmerman and McNicol 1988). Moose avoided dense canopies at night in all seasons. Moose often bed in areas with more open canopies at night as a means of thermal relief through radiant heat loss

(McCann et al. 2016). In northeast Minnesota, full leaf-out in spring and summer likely provides dense canopies that offer some thermal relief regardless of cover type (McGraw et al. 2012). However, dense canopies limit the amount of light penetration at the ground level and so understory growth can be less available under denser canopies (Canham et al. 1994). Broken or sparse canopies that allow significant light penetration to the understory will support more abundant understory growth (Runkle 1981, Frelich et al. 1998), and therefore will be more attractive to moose within home ranges when food availability is the limiting factor.

We recognize that often there is a benefit to including interaction terms in candidate models of resource selection functions. In this case, an interaction term between cover type and LiDAR-based forest structural components may have further elucidated moose resource selection patterns. However, because there was little difference in the distributions of forest structural components among cover types (Fig. 3.3), we chose not to include an interaction term. Future studies could consider exploring potential interactions between cover types and forest structural components to better understand resource selection patterns among moose. However, we caution that potential significant interactions be interpreted with caution because results could be affected by uncertainty in the accuracy and composition of some cover types (Homer et al. 2015), especially uncertainty and variability in understory vegetation composition, which is not identified in the NLCD dataset. If interaction terms that include information about understory structure are included in future models of moose resource selection, we recommend field data collection of understory vegetation composition associated with different cover types.

Conclusions

While spring and fall are typically considered less important for moose habitat management, we suggest managers consider the importance of these seasons to moose health and nutritional condition. Our results suggest that moose need upland forest habitats with open canopies and dense understories in spring, when they are in poorest body condition. This time period is when snow cover is lost, exposing leaf litter and greening foliage that could be important for moose to survive the end of severe winters and meet the energetic demands of calving before full green-up occurs. In the fall, prolonged access to green forage allows moose to acquire and store additional energy that will sustain them through winter. Maintaining woody wetlands on the landscape could be important for moose overwinter survival.

Moose are thought to use clear-cuts, post-fire disturbances, and other disturbed areas that result in large areas of young, regenerating forests as foraging habitat (Irwin 1975, Courtois et al. 2002), and habitat management plans for moose often include recommendations for creation of more young forests (Minnesota Moose Research and Management Plan 2011). One important limitation of our study was that an analysis of forest disturbance use by moose was not done given accuracy limitations of existing forest disturbance datasets. Additional studies of moose resource selection should include stand age and disturbance data when it is available. In Minnesota, remotely sensed datasets that estimate stand age and type of disturbance are becoming available in the near future, and so we recommend that future habitat studies for moose in northeast Minnesota incorporate these data.

Table 3.1. Covariates used in seasonal, night/day, and behavior-specific RSF models for moose in northeast Minnesota. Land cover variables were derived from National Land Cover Database (NLCD 2011, Homer et al. 2015) and forest structure metrics were derived from Light Detection and Ranging (LiDAR) collected in 2011 for the region.

Predictor Variable	Proportion Available	Description
Cover Type		
Deciduous	14%	>20% total vegetation cover and >75% of trees shed foliage simultaneously because of seasonal change
Mixed Forest	16%	>20% total vegetation cover and neither deciduous or conifer are >75% of canopy cover
Shrub	12%	>20% total vegetation cover and includes true shrubs and young trees
Conifer	16%	>20% total vegetation cover and >75% of tree species maintain leaves all year so that the canopy always maintains green foliage
Woody Wetlands	39%	>20% of vegetation cover is either forest or shrub and soil is periodically covered in water or saturated
Other	4%	Remaining cover types that, individually, comprise < 10% of the landscape; includes developed cover types, agriculture, and emergent wetlands
Canopy height	--	Height 75th percentile
Canopy cover	--	Percent of vegetation returns > 3 m
Understory density	--	Percent of vegetation returns 1 - 3 m

Table 3.2. Season dates by year. Seasons were identified by climate patterns (e.g., snowfall, first frost dates) and biological relevance to moose (e.g., localization during parturition). As a result, the dates may vary slightly from one year to the next, but allowed for pooling locations across years, by season.

Year	Season	Start Date	End Date	Days per season	Moose per season
2011	Winter	01/01/2011	04/23/2011	112	13
2011	Spring	04/24/2011	05/15/2011	21	13
2011	Summer	06/07/2011	09/05/2011	90	13
2011	Fall	09/06/2011	11/25/2011	80	10
2012	Winter	11/26/2011	03/16/2012	111	7
2012	Spring	03/17/2012	05/15/2012	59	6
2012	Summer	06/07/2012	09/14/2012	99	6
2012	Fall	09/15/2012	11/23/2012	69	5

Table 3.3. 95% kernel home range for moose in each season and year of the study based on locations collected at 2-hour intervals during the non-snow period (spring, summer, fall) and the snow period (winter). There was only one male remaining in the study during the 2012 snow season, and so an average value could not be computed.

Year	Season	Male Home Range (km^2) ± SE	Female Home Range (km^2) ± SE
2011	Non-snow period	70.38 (± 21.84)	21.21 (± 3.84)
2011	Snow period	22.36 (± 7.8)	22.34 (± 11.84)
2012	Non-snow period	56.26 (± 21.24)	27.12 (± 14.24)
2012	Snow period	245.14*	28.58 (± 7.81)

*this male had an unusually large home range, but was not migratory, moving throughout the home range within the 2012 snow period.

Table 3.4. Behavior bouts lengths and mean activity level for each behavior, in each season. Start and end points for active and inactive bouts were identified using change point analysis with the PELT algorithm and activity level values.

Season	Mean Length Active Bout (±SEM)	Mean Length Inactive Bout (±SEM)
Winter	128 min (± 1 min)	182 min (± 1 min)
Spring	250 min (± 11 min)	182 min (± 4 min)
Summer	69 min (± 0.5 min)	104 min (± 0.6 min)
Fall	76 min (± 1 min)	130 min (± 1.5 min)

Table 3.5. Akaike's Information Criterion (AIC) values for moose resource selection function models used in model selection during spring and summer, at day and night, and for each behavior with each season. Model variables were land cover (cover), canopy height (h75), canopy density (st1), understory density (st2). K is the number of model parameters, ΔAIC is $AIC_i - AIC_{min}$, and *w* is $\exp(-0.5 * \Delta AIC) / \sum \exp(-0.5 * \Delta AIC)$.

Variables	K	AIC	ΔAIC	*w*
		Spring, Season		
cover, h75, st1, st2	4	152340	0	1.00
cover, st1, st2	3	152370	30	0.00
cover, st2	3	152475	135	0.00
cover, h75, st2	2	152476	136	0.00
cover, st1	3	153101	761	0.00
st1, st2	2	153262	922	0.00
h75, st1, st2	2	153330	990	0.00
h75, st2	2	153345	1005	0.00
st2	1	153355	1015	0.00
cover, h75	3	153374	1034	0.00
cover	1	153670	1330	0.00
cover, h75, st1	2	153672	1332	0.00
h75, st1	2	154390	2050	0.00
h75	1	154413	2073	0.00
st1	1	154560	2220	0.00
		Spring, Active		
cover, h75, st1, st2	4	30024	0	1.00
cover, st1, st2	3	30064	40	0.00
cover, st2	3	30069	45	0.00
cover, h75	3	30184	160	0.00
h75, st1, st2	2	30185	161	0.00
cover, h75, st2	2	30282	258	0.00
cover, h75, st1	2	30545	521	0.00
cover	1	30618	594	0.00
cover, st1	3	30771	747	0.00
st1, st2	2	30781	757	0.00
h75, st2	2	30849	825	0.00
h75	1	31015	991	0.00
h75, st1	2	31016	992	0.00
st2	1	31047	1023	0.00
st1	1	31345	1321	0.00
		Spring, Inactive		
Variables	K	AIC	ΔAIC	*w*
cover, h75, st1, st2	4	23962	0	0.62
cover, st2	3	23963	1	0.38
cover, st1, st2	3	23982	20	0.00
cover, h75, st2	2	23982	20	0.00
h75, st1, st2	2	23985	23	0.00
cover, h75	3	24018	56	0.00
cover, h75, st1	2	24087	125	0.00
cover	1	24088	126	0.00
h75, st2	2	24214	252	0.00
cover, st1	3	24215	253	0.00

Variables	K	AIC	ΔAIC	*w*
st1, st2	2	24229	267	0.00
st2	1	24232	270	0.00
h75, st1	2	24263	301	0.00
h75	1	24309	347	0.00
st1	1	24387	425	0.00
		Spring, Day		
cover, h75, st1, st2	4	86421	0	0.49
cover, st1, st2	3	86421	0	0.49
cover, st2	3	86428	7	0.01
cover, h75, st2	2	86441	20	0.00
h75, st1, st2	2	86938	517	0.00
cover, st1	3	87023	602	0.00
h75, st2	2	87023	602	0.00
st1, st2	2	87060	639	0.00
st2	1	87105	684	0.00
cover, h75, st1	2	87234	813	0.00
cover, h75	3	87263	842	0.00
cover	1	87391	970	0.00
h75, st1	2	87734	1313	0.00
st1	1	87938	1517	0.00
h75	1	88073	1652	0.00
		Spring, Night		
cover, h75, st1, st2	4	65299	0	1.00
cover, st1, st2	3	65362	63	0.00
cover, st1	3	65567	268	0.00
cover, st2	3	65735	436	0.00
st1, st2	2	65747	448	0.00
cover, h75, st2	2	65774	475	0.00
h75, st1, st2	2	65803	504	0.00
cover, h75, st1	2	65866	567	0.00
cover, h75	3	65897	598	0.00
cover	1	66071	772	0.00
h75, st1	2	66178	879	0.00
h75, st2	2	66185	886	0.00
st1	1	66186	887	0.00
st2	1	66196	897	0.00
h75	1	66341	1042	0.00
		Summer, Season		
Variables	K	AIC	ΔAIC	*w*
cover, h75, st1, st2	4	109275	0	1.00
h75, st1, st2	2	109328	53	0.00
cover, st1, st2	3	109546	271	0.00
cover, h75, st1	2	109546	271	0.00
cover, st2	3	109634	359	0.00
cover, h75	3	109731	456	0.00
cover, st1	3	110937	1662	0.00
h75, st1	2	110960	1685	0.00
st1, st2	2	110992	1717	0.00
st1	1	110995	1720	0.00

Variables	K	AIC	ΔAIC	*w*
cover, h75, st2	2	111022	1747	0.00
cover	1	111043	1768	0.00
h75, st2	2	111315	2040	0.00
h75	1	111377	2102	0.00
st2	1	112135	2860	0.00
		Summer, Active		
cover, h75, st1, st2	4	114174	0	1.00
cover, h75, st1	2	114262	88	0.00
cover, st1, st2	3	114343	169	0.00
cover, st1	3	114369	195	0.00
cover, h75, st2	2	115310	1136	0.00
cover, h75	3	115517	1343	0.00
h75, st1, st2	2	116441	2267	0.00
st1, st2	2	116458	2284	0.00
h75, st1	2	116511	2337	0.00
st1	1	116512	2338	0.00
h75, st2	2	117499	3325	0.00
cover, st2	3	117596	3422	0.00
cover	1	117597	3423	0.00
h75	1	117692	3518	0.00
st2	1	119065	4891	0.00
		Summer, Inactive		
cover, h75, st1, st2	4	178617	0	0.88
cover, st2	3	178621	4	0.12
cover, h75, st2	2	178662	45	0.00
cover, h75	3	178662	45	0.00
cover, h75, st1	2	178663	46	0.00
cover, st1, st2	3	179225	608	0.00
h75, st1, st2	2	179377	760	0.00
h75	1	180419	1802	0.00
cover, st1	3	181641	3024	0.00
st1, st2	2	181653	3036	0.00
h75, st2	2	181723	3106	0.00
st1	1	181727	3110	0.00
h75, st1	2	181839	3222	0.00
st2	1	181929	3312	0.00
cover	1	182524	3907	0.00
		Summer, Day		
cover, h75, st1, st2	4	447782	0	1.00
h75, st1, st2	2	447976	194	0.00
cover, st2	3	449137	1355	0.00
cover, h75	3	449382	1600	0.00
cover, st1, st2	3	450402	2620	0.00
cover, h75, st2	2	450471	2689	0.00
cover	1	451732	3950	0.00
cover, h75, st1	2	451734	3952	0.00
cover, st1	3	452219	4437	0.00
h75, st1	2	452683	4901	0.00
st1, st2	2	453485	5703	0.00

Variables	K	AIC	ΔAIC	*w*
h75, st2	2	453851	6069	0.00
st2	1	454014	6232	0.00
h75	1	454451	6669	0.00
st1	1	454913	7131	0.00
		Summer, Day		
cover, h75, st1, st2	4	240497	0	1.00
cover, st1, st2	3	240520	23	0.00
h75, st1, st2	2	241975	1478	0.00
cover, h75, st1	2	242088	1591	0.00
cover, st1	3	246906	6409	0.00
st1, st2	2	247050	6553	0.00
h75, st1	2	248226	7729	0.00
st1	1	249047	8550	0.00
cover, st2	3	249538	9041	0.00
cover, h75	3	252804	12307	0.00
h75, st2	2	257378	16881	0.00
cover, h75, st2	2	258260	17763	0.00
cover	1	258982	18485	0.00
h75	1	260993	20496	0.00
st2	1	265480	24983	0.00

Table 3.6. Akaike's Information Criterion (AIC) values for moose resource selection function models used in model selection during fall and winter, at day and night, and for each behavior with each season. Model variables were land cover (cover), canopy height (h75), canopy density (st1), understory density (st2). K is the number of model parameters, ΔAIC is $AIC_i - AIC_{min}$, and *w* is $\exp(-0.5 * \Delta AIC) / \sum \exp(-0.5 * \Delta AIC)$.

Variables	K	AIC	ΔAIC	*w*
		Fall, Seasonal		
h75, st1, st2	2	62591	0	0.62
cover, h75, st1, st2	4	62592	1	0.38
cover, st1, st2	3	62784	193	0.00
cover, h75, st1	2	62833	242	0.00
cover, st1	3	63286	695	0.00
h75, st1	2	63292	701	0.00
cover, st2	3	63467	876	0.00
cover, h75	3	63486	895	0.00
st1, st2	2	63642	1051	0.00
st1	1	63771	1180	0.00
h75, st2	2	64138	1547	0.00
h75	1	64151	1560	0.00
cover, h75, st2	2	65695	3104	0.00
cover	1	65865	3274	0.00
st2	1	67773	5182	0.00
		Fall, Active		
cover, h75, st1, st2	4	50254	0	0.50
cover, h75, st1	2	50254	0	0.50
cover, st1, st2	3	50373	119	0.00
cover, st1	3	50413	159	0.00
h75, st1, st2	2	50582	328	0.00
h75, st1	2	50585	331	0.00
st1, st2	2	50761	507	0.00
st1	1	50828	574	0.00
cover, h75, st2	2	51562	1308	0.00
cover, h75	3	51595	1341	0.00
h75, st2	2	51965	1711	0.00
h75	1	52011	1757	0.00
cover, st2	3	54347	4093	0.00
cover	1	54507	4253	0.00
st2	1	56215	5961	0.00
		Fall, Inactive		
cover, h75, st1, st2	4	91289	0	0.97
cover, h75, st1	2	91296	7	0.03
cover, st1, st2	3	91498	209	0.00
cover, st1	3	91504	215	0.00
h75, st1	2	92321	1032	0.00
h75, st1, st2	2	92323	1034	0.00
cover, h75, st2	2	92618	1329	0.00
st1, st2	2	92639	1350	0.00
st1	1	92697	1408	0.00
cover, h75	3	92721	1432	0.00
h75, st2	2	93738	2449	0.00
h75	1	93806	2517	0.00
cover, st2	3	96152	4863	0.00
cover	1	96271	4982	0.00
st2	1	99152	7863	0.00

Variables	K	AIC	ΔAIC	*w*
		Fall, Day		
cover, h75, st1, st2	4	148982	0	1.00
cover, h75, st2	2	149034	52	0.00
cover, h75, st1	2	149146	164	0.00
cover, h75	3	149180	198	0.00
cover, st1, st2	3	149407	425	0.00
cover, st1	3	149940	958	0.00
cover, st2	3	150142	1160	0.00
Cover	1	151009	2027	0.00
h75, st1, st2	2	152305	3323	0.00
h75, st2	2	152323	3341	0.00
h75, st1	2	152609	3627	0.00
h75	1	152611	3629	0.00
st1, st2	2	153225	4243	0.00
st1	1	154272	5290	0.00
st2	1	154470	5488	0.00
		Fall, Night		
cover, h75, st1, st2	4	155042	0	1.00
cover, h75, st1	2	155055	13	0.00
cover, st1, st2	3	155522	480	0.00
cover, st1	3	155548	506	0.00
h75, st1, st2	2	155989	947	0.00
h75, st1	2	156000	958	0.00
st1, st2	2	156670	1628	0.00
st1	1	156731	1689	0.00
cover, h75, st2	2	162112	7070	0.00
cover, h75	3	162739	7697	0.00
h75, st2	2	163140	8098	0.00
h75	1	163937	8895	0.00
cover, st2	3	175500	20458	0.00
cover	1	175621	20579	0.00
st2	1	182735	27693	0.00
		Winter, Season		
cover, h75, st1, st2	4	52084	0	0.78
h75, st1, st2	2	52087	3	0.17
cover, st1, st2	3	52091	7	0.02
cover, h75, st1	2	52091	7	0.02
cover	1	52123	39	0.00
cover, h75	3	52124	40	0.00
cover, h75, st2	2	52125	41	0.00
cover, st2	3	52125	41	0.00
cover, st1	3	52829	745	0.00
h75, st1	2	52835	751	0.00
h75	1	52863	779	0.00
h75, st2	2	52864	780	0.00
st1	1	52955	871	0.00
st1, st2	2	52956	872	0.00
st2	1	52961	877	0.00
		Winter, Active		
cover, h75, st1, st2	4	101943	0	1.00
cover, st1, st2	3	102063	120	0.00
cover, h75, st1	2	102072	129	0.00
cover, st1	3	102364	421	0.00
cover, h75, st2	2	102942	999	0.00

Variables	K	AIC	ΔAIC	*w*
cover, h75	3	102944	1001	0.00
h75, st1, st2	2	103445	1502	0.00
st1, st2	2	103494	1551	0.00
h75, st1	2	103559	1616	0.00
cover, st2	3	103706	1763	0.00
st1	1	103726	1783	0.00
cover	1	103735	1792	0.00
h75, st2	2	104562	2619	0.00
h75	1	104578	2635	0.00
st2	1	105348	3405	0.00
		Winter, Inactive		
cover, h75, st1, st2	4	152824	0	1.00
cover, st1, st2	3	152888	64	0.00
cover, h75, st1	2	153138	314	0.00
cover, st1	3	153423	599	0.00
h75, st1, st2	2	154647	1823	0.00
st1, st2	2	154681	1857	0.00
h75, st1	2	154933	2109	0.00
cover, h75, st2	2	154972	2148	0.00
cover, h75	3	154974	2150	0.00
st1	1	155146	2322	0.00
cover, st2	3	156015	3191	0.00
cover	1	156065	3241	0.00
h75, st2	2	156885	4061	0.00
h75	1	156899	4075	0.00
st2	1	158156	5332	0.00
		Winter, Day		
cover, st1, st2	3	243058	0	0.73
cover, h75, st1, st2	4	243060	2	0.27
cover, h75, st1	2	243866	808	0.00
cover, st1	3	244033	975	0.00
cover, h75, st2	2	245486	2428	0.00
h75, st1, st2	2	245517	2459	0.00
cover, h75	3	245557	2499	0.00
st1, st2	2	245592	2534	0.00
cover, st2	3	246024	2966	0.00
cover	1	246290	3232	0.00
h75, st1	2	246335	3277	0.00
st1	1	246356	3298	0.00
h75, st2	2	247809	4751	0.00
h75	1	247888	4830	0.00
st2	1	248084	5026	0.00
		Winter, Night		
cover, h75, st1, st2	4	289452	0	1.00
cover, st1, st2	3	289543	91	0.00
cover, h75, st1	2	290708	1256	0.00
cover, st1	3	291539	2087	0.00
h75, st1, st2	2	293893	4441	0.00
st1, st2	2	293897	4445	0.00
h75, st1	2	295057	5605	0.00
st1	1	295513	6061	0.00
cover, h75, st2	2	296444	6992	0.00
cover, h75	3	296457	7005	0.00
cover, st2	3	299920	10468	0.00

Variables	K	AIC	ΔAIC	*w*
cover	1	300094	10642	0.00
h75, st2	2	301384	11932	0.00
h75	1	301445	11993	0.00
st2	1	305136	15684	0.00

Table 3.7. K-fold cross validation results for top models for each season and scale of selection identified using AIC. We used 5-folds in the cross validation and tested goodness of fit with the Spearman rank correlation test.

	Winter		Spring		Summer		Fall	
Model	$\bar{r_s}$	P-value	$\bar{r_s}$	P-value	$\bar{r_s}$	P-value	$\bar{r_s}$	P-value
Seasonal Pooled	0.98	<0.01	0.92	<0.01	0.96	<0.01	0.98	<0.01
Day	0.99	<0.01	0.87	<0.01	0.87	<0.01	0.90	<0.01
Night	0.99	<0.01	0.51	<0.01	0.97	<0.01	0.95	<0.01
Active	0.98	<0.01	0.78	<0.01	0.97	<0.01	0.91	<0.01
Inactive	0.94	<0.01	0.75	<0.01	0.90	<0.01	0.95	<0.01

Table 3.8. Coefficient values (β) and standard errors for each season, and day and night and each behavior within each season obtained after fitting the top resource selection model as identified using AIC. All coefficients were included in each seasonal, day/night, and behavioral model.

			Winter		
Coefficient	All	Day	Night	Active	Inactive
Cover Type					
Deciduous	0.31 ± 0.03	0.22 ± 0.04	0.37 ± 0.03	0.51 ± 0.06	0.47 ± 0.06
Conifer	0.17 ± 0.02	0.22 ± 0.03	0.21 ± 0.03	0.21 ± 0.06	0.11 ± 0.06
Mixed Forest	0.62 ± 0.02	0.59 ± 0.03	0.69 ± 0.03	0.64 ± 0.05	0.62 ± 0.05
Shrub	0.61 ± 0.02	0.45 ± 0.04	0.78 ± 0.03	0.66 ± 0.05	0.81 ± 0.06
Other	-0.32 ± 0.05	-0.76 ± 0.08	-0.07 ± 0.06	-0.20 ± 0.11	-0.10 ± 0.10
Canopy Height	-0.04 ± 0.01	-0.05 ± 0.01	-0.08 ± 0.01	-0.14 ± 0.02	-0.10 ± 0.02
Canopy Cover	-0.40 ± 0.01	-0.30 ± 0.01	-0.50 ± 0.01	-0.29 ± 0.02	-0.31 ± 0.02
Understory Cover	0.18 ± 0.01	0.16 ± 0.01	0.19 ± 0.01	0.08 ± 0.02	0.12 ± 0.02
			Spring		
Cover Type					
Deciduous	0.26 ± 0.04	0.36 ± 0.07	0.35 ± 0.07	0.75 ± 0.12	0.18 ± 0.14
Conifer	-0.16 ± 0.04	-0.13 ± 0.07	-0.12 ± 0.07	-0.43 ± 0.11	-0.47 ± 0.12
Mixed Forest	0.04 ± 0.04	0.18 ± 0.07	0.16 ± 0.07	0.04 ± 0.09	0 ± 0.11
Shrub	-0.29 ± 0.05	-0.18 ± 0.07	-0.24 ± 0.07	-1 ± 0.12	-0.62 ± 0.13
Other	-0.27 ± 0.09	-0.22 ± 0.12	-0.06 ± 0.12	-0.3 ± 0.15	-0.54 ± 0.2
Canopy Height	0.05 ± 0.02	0.11 ± 0.03	0.07 ± 0.03	-0.18 ± 0.05	-0.05 ± 0.06
Canopy Cover	-0.09 ± 0.02	-0.31 ± 0.03	-0.3 ± 0.03	-0.1 ± 0.05	0.01 ± 0.05
Understory Cover	0.26 ± 0.02	0.3 ± 0.03	0.28 ± 0.03	0.28 ± 0.05	0.13 ± 0.05
			Summer		
Cover Type					
Deciduous	-0.33 ± 0.02	0.52 ± 0.03	0.86 ± 0.04	0.58 ± 0.05	0.73 ± 0.04
Conifer	0.64 ± 0.02	0.25 ± 0.03	0.54 ± 0.05	0.48 ± 0.05	0.27 ± 0.04
Mixed Forest	0.32 ± 0.02	0.57 ± 0.03	1.06 ± 0.04	0.80 ± 0.05	0.65 ± 0.04
Shrub	0.73 ± 0.02	0.19 ± 0.03	0.80 ± 0.04	0.56 ± 0.05	0.48 ± 0.04
Other	0.43 ± 0.02	-0.59 ± 0.06	0.01 ± 0.07	-0.38 ± 0.09	-0.37 ± 0.07
Canopy Height	-0.27 ± 0.04	-0.26 ± 0.01	0.00 ± 0.02	-0.16 ± 0.03	-0.21 ± 0.02
Canopy Cover	-0.21 ± 0.01	0.11 ± 0.01	-0.75 ± 0.02	-0.35 ± 0.02	-0.09 ± 0.02
Understory Cover	-0.18 ± 0.01	0.08 ± 0.01	-0.23 ± 0.01	-0.09 ± 0.02	0.01 ± 0.01
			Fall		
Cover Type					
Deciduous	-0.78 ± 0.04	-1.03 ± 0.05	-0.51 ± 0.05	-0.47 ± 0.09	-0.83 ± 0.07
Conifer	-0.42 ± 0.03	-0.69 ± 0.05	-0.10 ± 0.05	-0.27 ± 0.09	-0.57 ± 0.07
Mixed Forest	-0.27 ± 0.03	-0.59 ± 0.04	0.17 ± 0.05	-0.03 ± 0.08	-0.42 ± 0.06
Shrub	-0.10 ± 0.03	-0.41 ± 0.04	0.23 ± 0.04	0.17 ± 0.07	-0.19 ± 0.05
Other	-0.45 ± 0.05	-0.85 ± 0.08	-0.18 ± 0.07	-0.18 ± 0.11	-0.64 ± 0.08
Canopy Height	-0.26 ± 0.02	-0.20 ± 0.02	-0.24 ± 0.02	-0.24 ± 0.04	-0.21 ± 0.03
Canopy Cover	-0.42 ± 0.02	-0.04 ± 0.02	-0.85 ± 0.02	-0.64 ± 0.04	-0.46 ± 0.03
Understory Cover	-0.01 ± 0.01	0.11 ± 0.02	-0.02 ± 0.02	0.05 ± 0.03	-0.05 ± 0.02

Table 3.9. The correlation of coefficient values between night and day, and between active and inactive behaviors within a season.

	Correlation of Coefficient Value within Seasons: Day vs. Night and Active vs. Inactive			
Season	Day	Night	Active	Inactive
Winter	0.92	0.97	0.96	0.95
Spring	0.90	0.86	0.88	0.92
Summer	-0.03	0.45	0.38	0.16
Fall	0.74	0.61	0.76	0.95

Table 3.10. The average proportion of cover types (+/- SEM) used by moose and available to moose within 95% kernel home ranges during summer and winter in 2011 and 2012.

	Summer				Winter			
	2011		2012		2011		2012	
Cover Type	Used	Available	Used	Available	Used	Available	Used	Available
Conifer	14 (3)	16 (2)	10 (3)	14 (2)	18 (5)	19 (3)	9 (3)	15 (2)
Deciduous	19 (7)	15 (5)	17 (7)	15 (6)	14 (5)	14 (5)	16 (7)	14 (5)
Mixed Forest	20 (4)	16 (3)	21 (5)	15 (3)	29 (7)	19 (4)	12 (3)	14 (2)
Other	3 (1)	4 (1)	3 (1)	3 (1)	1 (1)	2 (1)	4 (1)	4 (1)
Shrub	14 (4)	11 (2)	19 (5)	13 (3)	10 (4)	9 (3)	26 (5)	16 (6)
Woody Wetlands	30 (6)	37 (6)	30 (6)	41 (6)	29 (7)	37 (7)	39 (8)	42 (6)

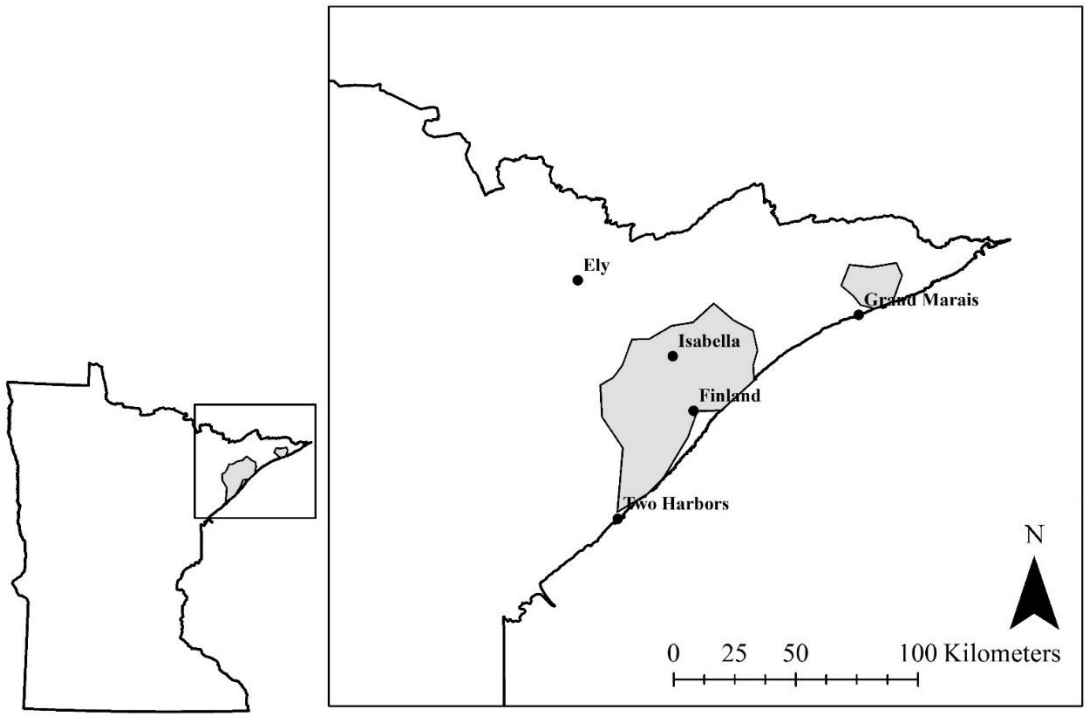


Figure 3.1. Moose resource selection study area in northeast Minnesota. Boundaries of the study area (gray polygons) were established by pooling moose GPS collar locations and drawing a 100% MCP around the two locations where moose were collared, Isabella, MN and Grand Marais, MN.

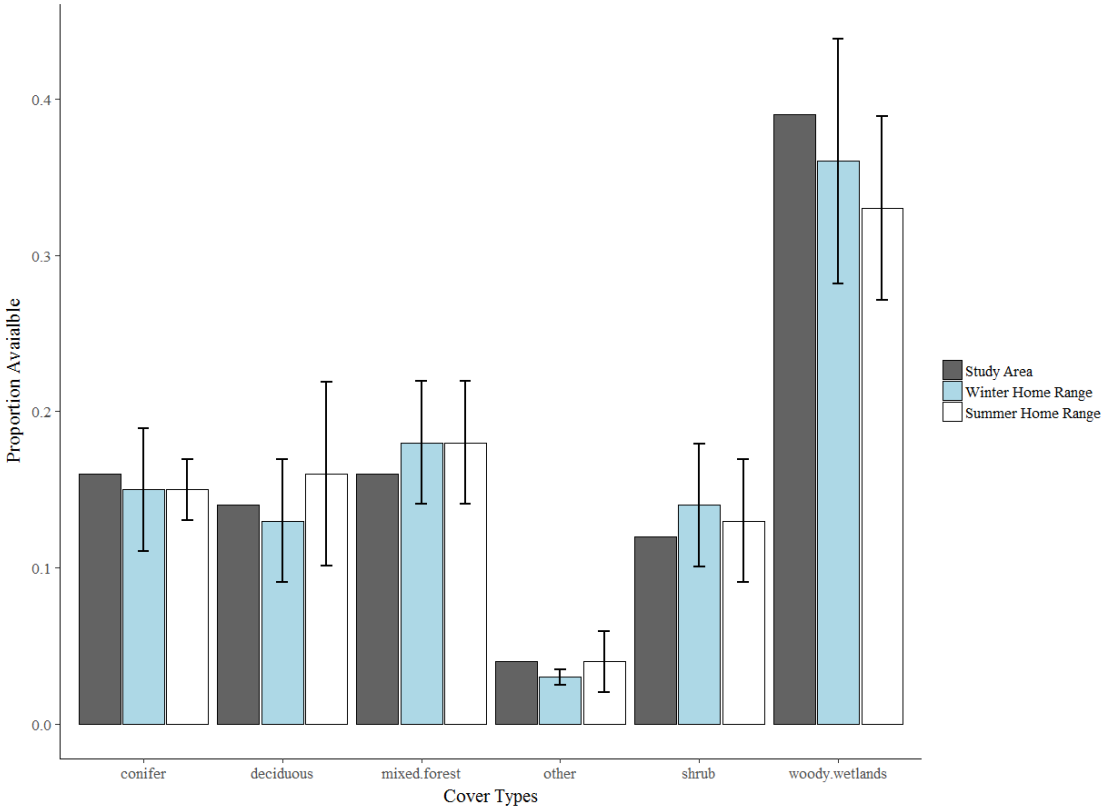


Figure 3.2. Proportion of land cover types available within spring/summer/fall (white) and winter (blue) home ranges. The proportion of land cover types available in the study area (the Isabella and Grand Marais study sites) is represented by dark gray bars. The error bars are 95% confidence limits.

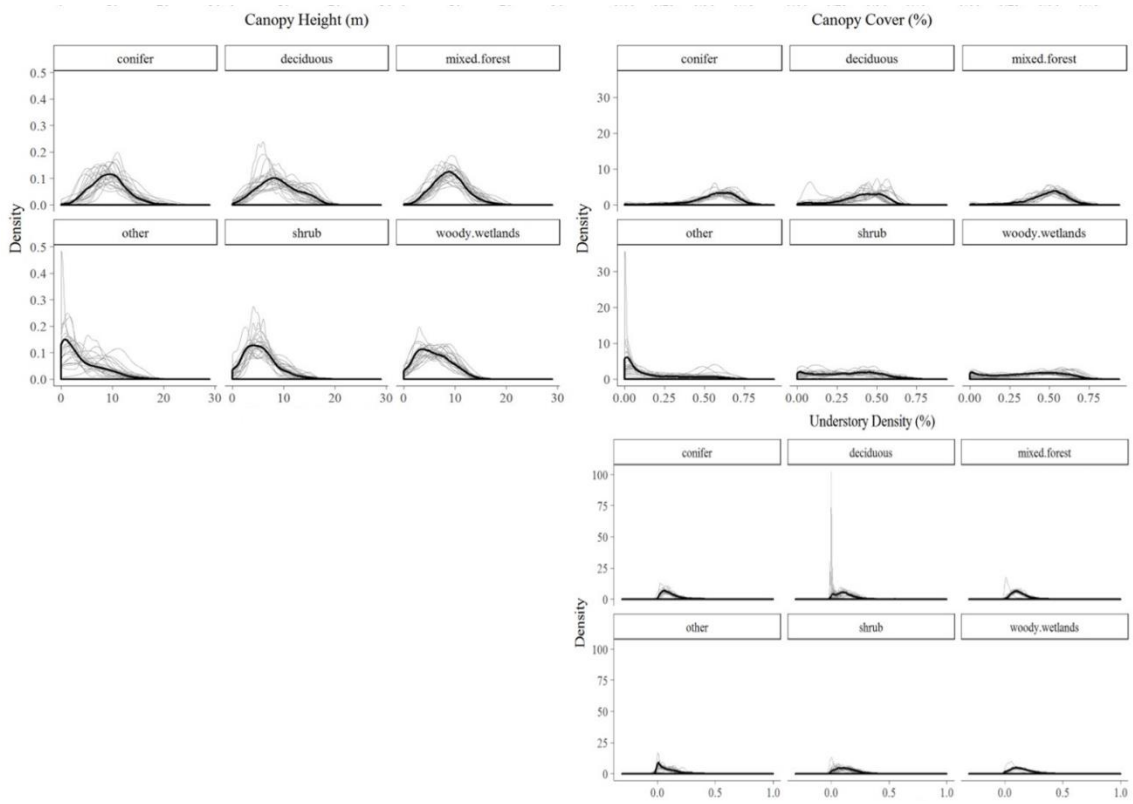


Figure 3.3. Distribution of canopy height, canopy cover, and understory density in each land cover type within moose home ranges. Thick black lines are the average canopy heights within each canopy height and thin gray lines represent the distribution of canopy heights within each cover type within each moose home range. The most variability in canopy cover distribution was observed in the deciduous cover type and the 'other' cover type.

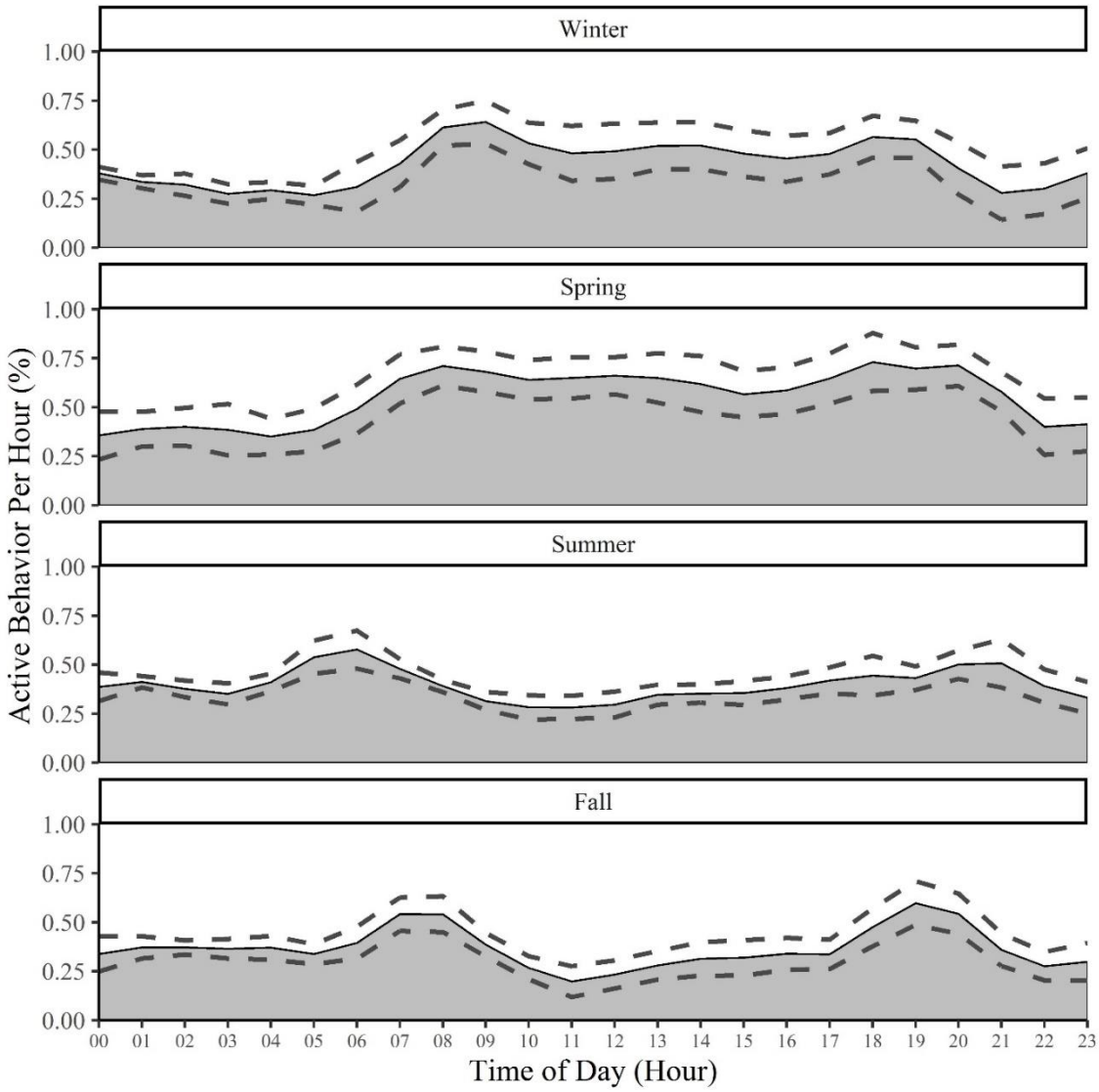


Figure 3.4. Diel activity patterns for each season. Gray areas represent the proportion of each hour that moose spent being active over the course of a 24-hour period. Dashed lines indicate the standard error of the mean for the proportion of each hour that moose spent being active. Moose activity peaked around sunrise and sunset in each season.

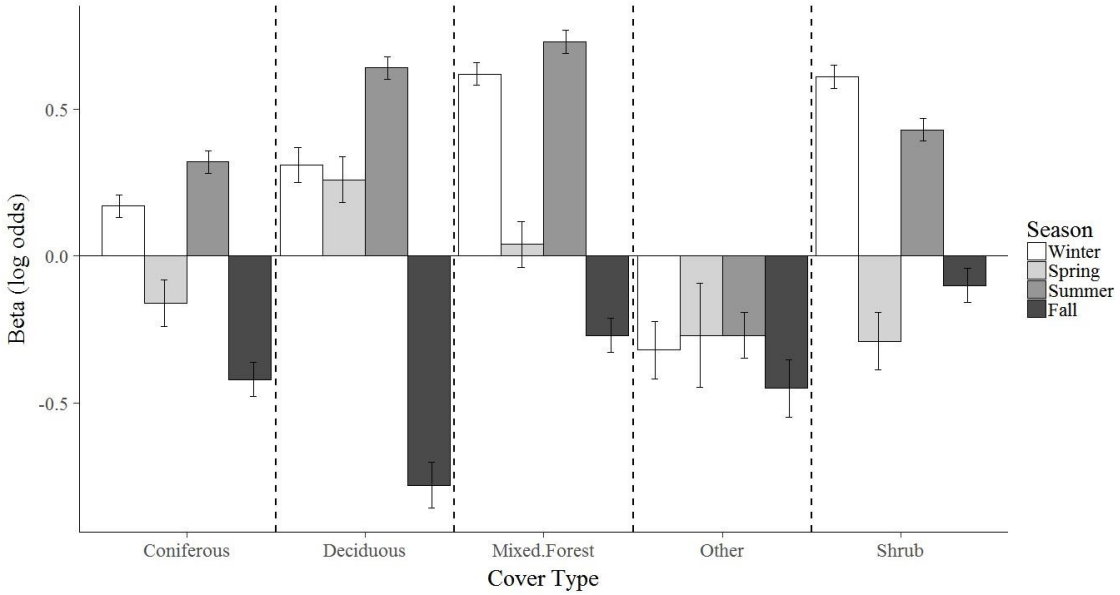


Figure 3.5. Seasonal relative probability of selection for land cover types by moose. The y-axis is the log odds of the relative probability of selection. Error bars are 95% confidence limits. Selection was significant if confidence limits did not include zero. The woody wetlands cover type was the reference category in seasonal models. Moose tended to select for forested cover types that provide food and shelter during summer and winter, while avoiding forested cover types in the fall.

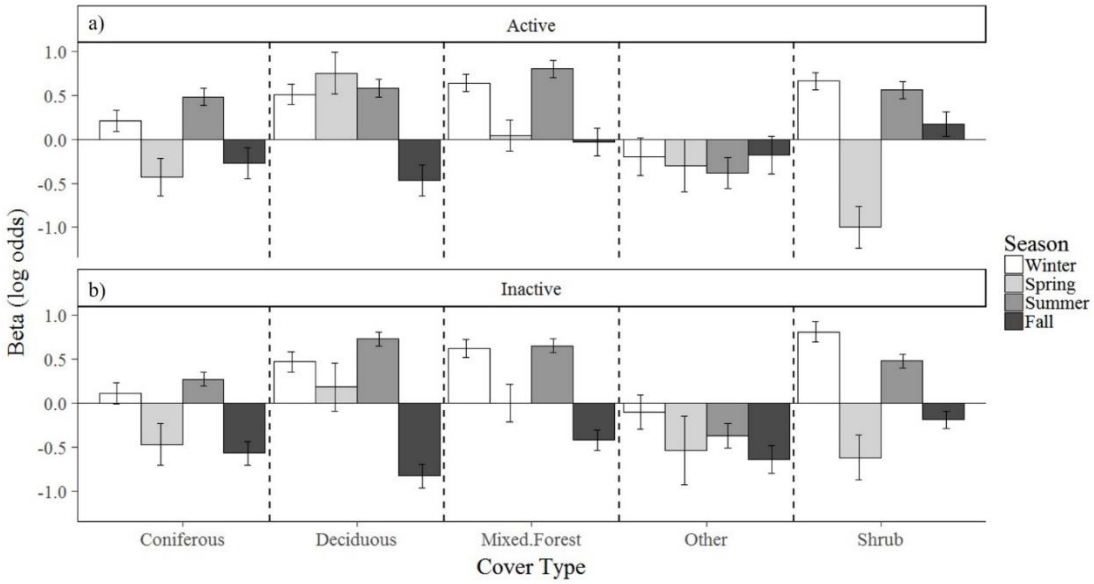


Figure 3.6. Relative probability of selection for land cover types by moose when active (a) and inactive (b) during each season. The y-axis is the log odds of the relative probability of selection. Error bars are 95% confidence limits. Selection was significant if confidence limits did not include zero. The woody wetlands cover type was the reference category for the cover type covariate in behavioral models for each season. Patterns generally reflected overall seasonal cover type selection patterns.

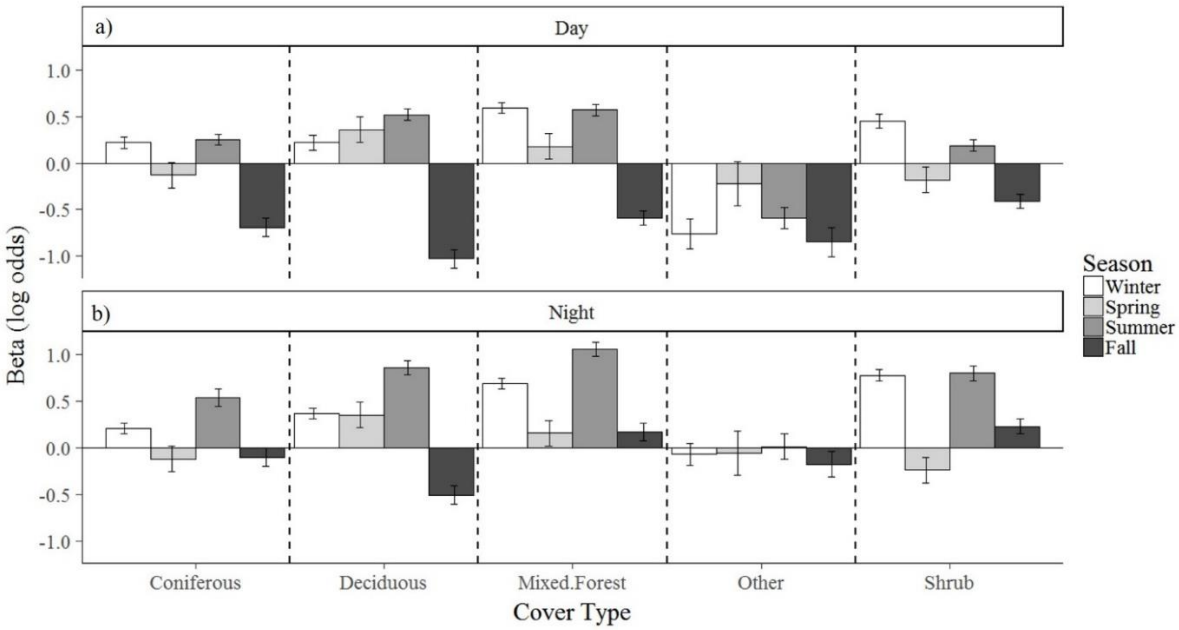


Figure 3.7. Relative probability of selection for land cover types by moose during the day (a) and at night (b) for each season. The y-axis is the log odds of the relative probability of selection. Error bars are 95% confidence limits. Selection was significant if confidence limits did not include zero. The woody wetlands cover type was the reference category for the cover type covariate in day/night models within each season. Day and night were determined daily using sunrise and sunset times at the centroid of the study area. Patterns generally reflected overall seasonal cover type selection patterns.

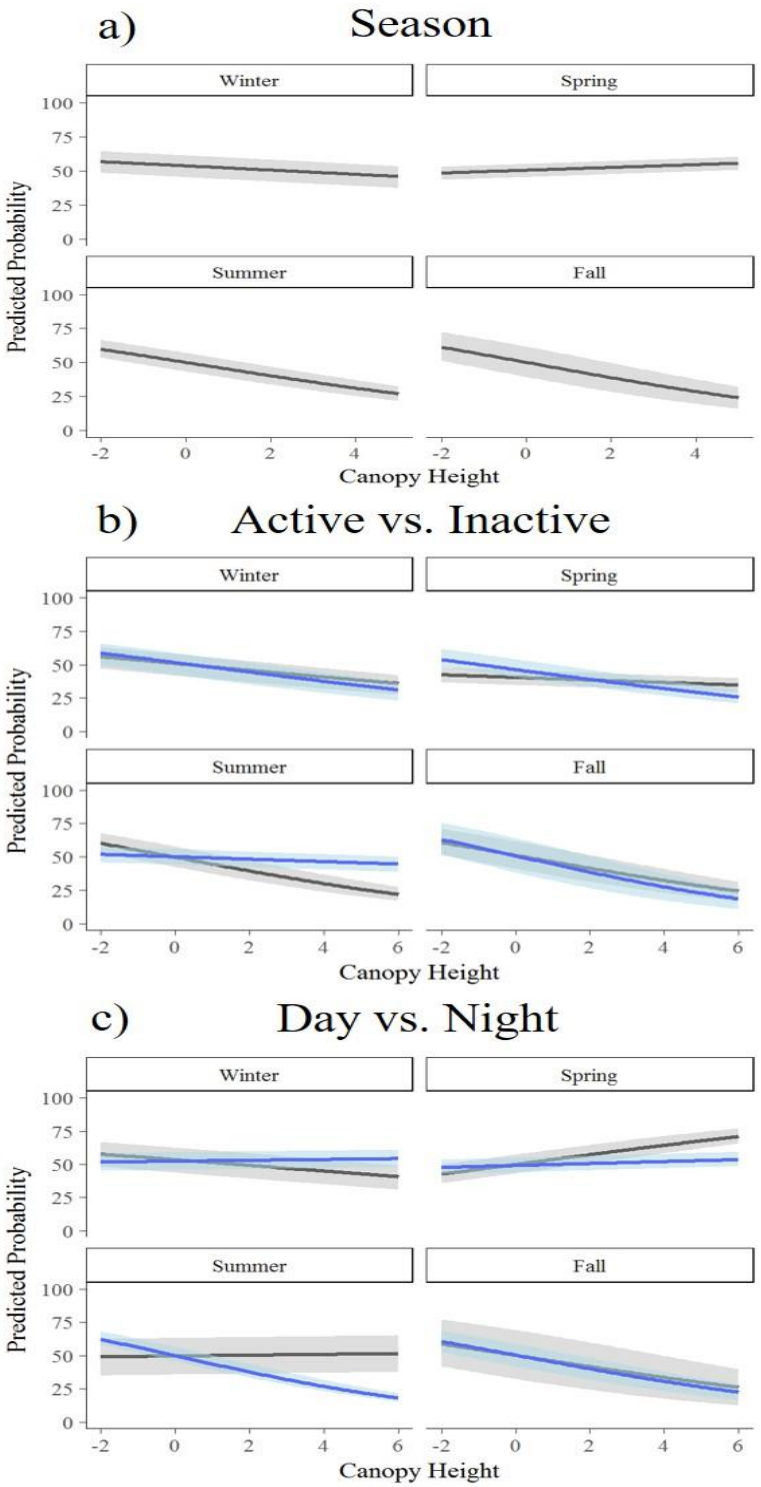


Figure 3.8. Relative probability of selection for canopy height during each season (a), within each season when moose were active (blue lines) or inactive (black lines, b), and within each season during the day (blue lines), and at night (black lines, c). Taller canopies were avoided most often in summer and the fall when active or inactive, during the day in summer, and during the day and at night during the fall.

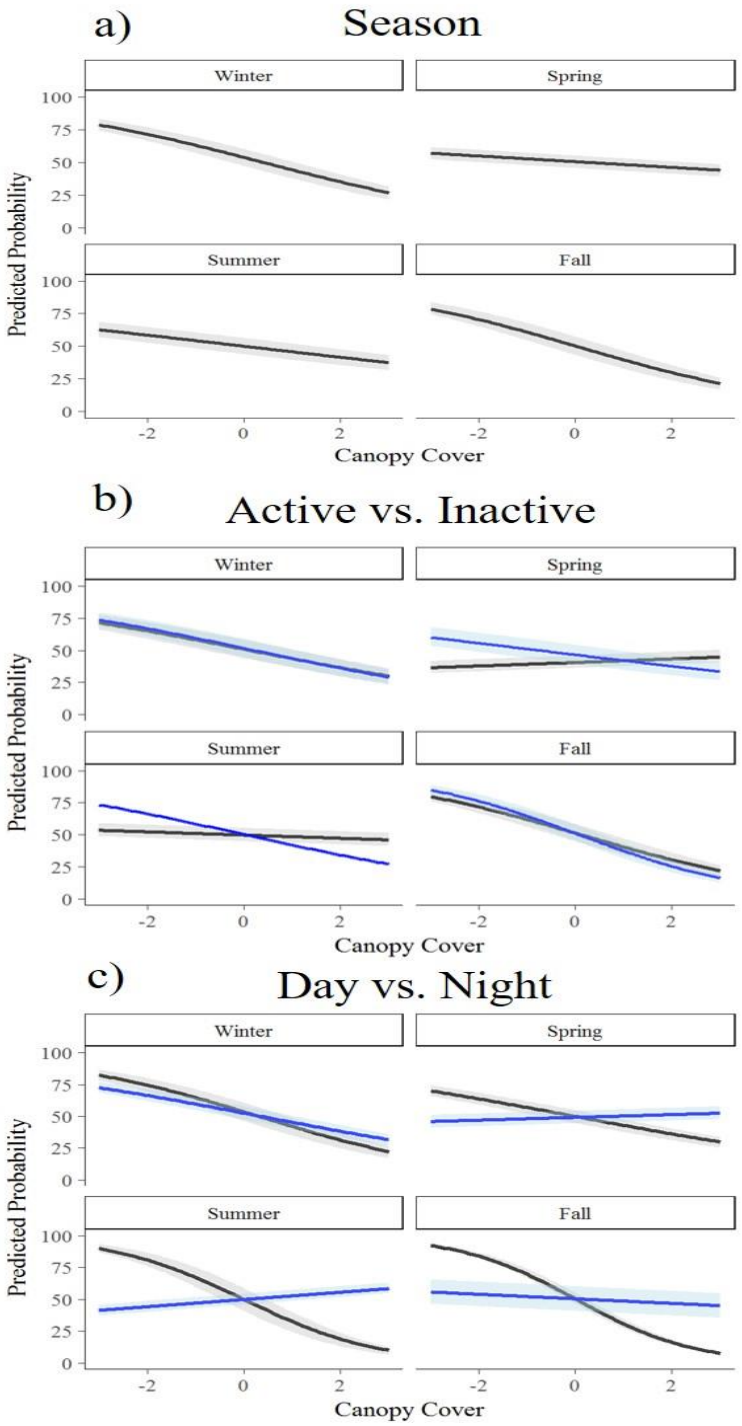


Figure 3.9. Relative probability of selection for canopy cover during each season (a), within each season when moose were active (blue lines) or inactive (black lines, b), and within each season during the day (blue lines), and at night (black lines, c). Moose generally avoided canopy cover in all seasons but selected for canopy cover during the day in spring and summer.

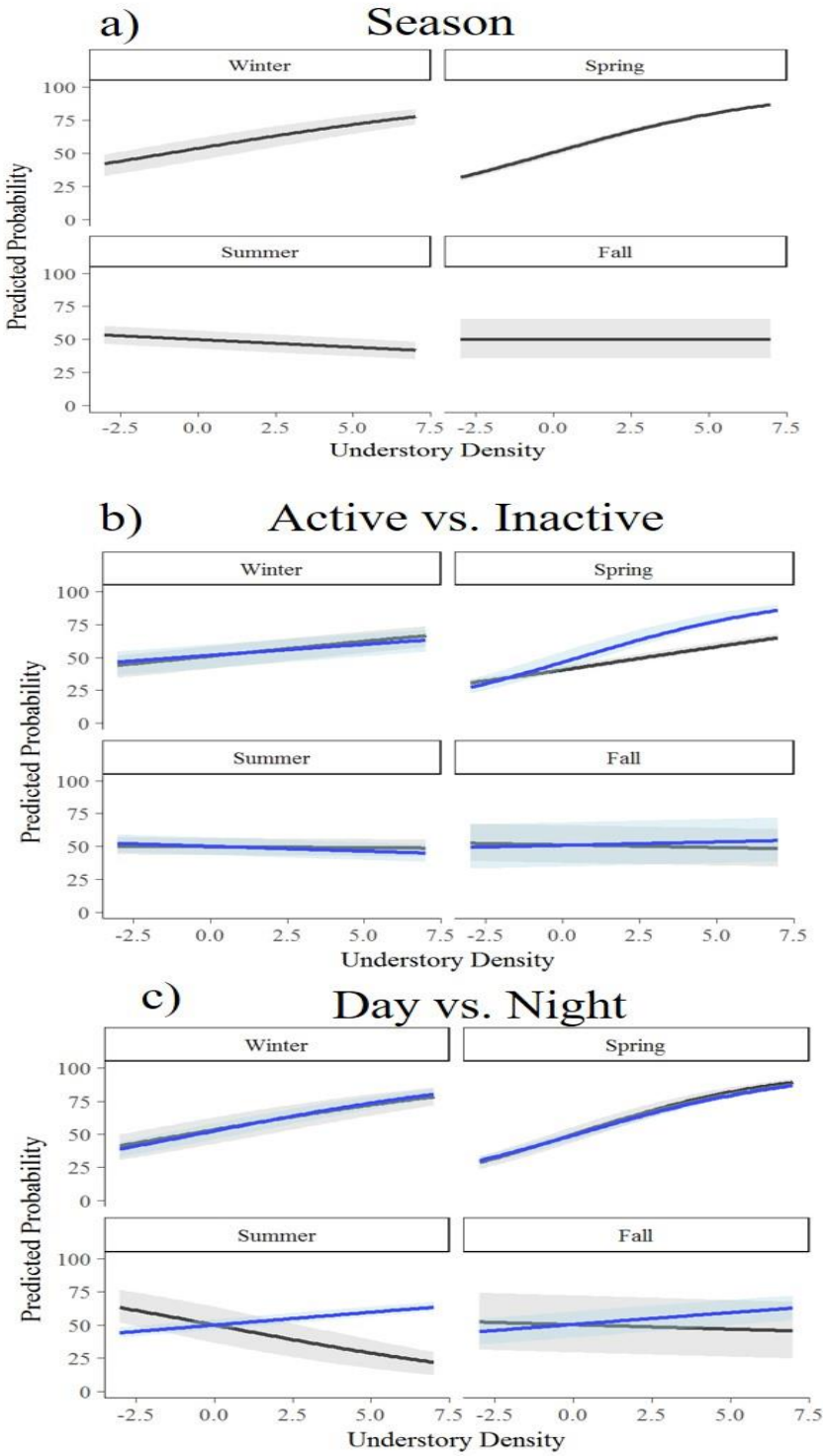


Figure 3.10. Relative probability of selection for dense understories during each season (a), within each season when moose were active (blue lines) or inactive (black lines, b), and within each season during the day (blue lines), and at night (black lines, c). Moose selected for denser understories in winter and spring regardless of behavior or time of day. Denser understories were selected during the day but avoided at night during the summer and fall. The lines for day and night during the spring are overlapping.

Chapter 4

Moose and white-tailed deer co-occurrence in northeast Minnesota

Preface

White-tailed deer (*Odocoileus virginianus*) are often implicated as the cause of moose (*Alces alces*) population declines by spreading disease. Where moose and deer ranges overlap, deer population densities are generally low, and their diets are browse-dominated and similar to moose diets, which could lead to biologically significant interaction and disease transmission. We quantified the relative probability of co-occurrence between moose and deer in northeast Minnesota using Resource Selection Functions. The relative probability of co-occurrence between moose and deer was estimated seasonally, to identify shared habitats that could lead to competition for forage resources and disease transmission. We also estimated the relative probability of co-occurrence between moose and deer that could lead to parasite-mediated competitive interactions by estimating occurrence of deer at an annual scale and during winter when deer shed the most *Parelaphostrongylus tenuis* larvae, while also estimating moose occurrence when deer were active in snow-free periods when exposure to *P. tenuis* could lead to infection. We found that moose and deer were most likely to co-occur in habitats that provide forage at all times of the year. We also found that mutual avoidance of habitat, such as wetlands and conifer, could contribute to a limited area where increased interaction on the landscape would be expected. By concentrating moose and deer into the same habitats, shared selection and avoidance of resources could lead to higher effective deer densities in areas of overlap than are estimated at a coarser spatial scale, and that could lead to increased risk of disease transmission to moose. Management actions to improve habitat for moose, which generally involve creation of foraging habitat, in regions where deer are present are likely to increase the potential for interactions between moose and deer.

Key words: *Alces alces*, co-occurrence, disease transmission, Minnesota, moose, *Odocoileus virginianus*, *Parelaphostrongylus tenuis*, white-tailed deer

Introduction

A long-held tenet of ecology is that similar species can coexist when there is some form of niche differentiation, which is usually the result of evolutionary processes that reduce or eliminate significant competition (Gause 1934, Hardin 1960). Ecological niche differentiation typically occurs through partitioning of resources, separation in space, or avoidance in time (Gause 1934, Hardin 1960, Wereszczuk and Zalewski 2015). When niche differentiation has not developed between similar species, several types of competition can occur and can lead to extirpation of the less effective competitor. For example, interference competition occurs when direct interactions disproportionately affect one species (Price et al. 1986), whereas resource competition arises when one species restricts access of the other species to a common resource (Price et al. 1986).

A type of competition that has received more attention recently is parasite-mediated competition, which occurs when a parasite is hosted by different species but has a more negative impact on one host species (Price et al. 1986). Parasite-mediated competition is an indirect form of competition and operates differently from direct types of interaction because the parasite has an ecology of its own (Price et al. 1986). In parasite-mediated systems, transmission is the driver of host-parasite interactions and the patterns of transmission depend on the density of each species, on how infectious the parasite is, and on how the susceptible hosts interact both socially and spatially (Ferrari et al. 2011). Disease risk is tightly linked with interaction between hosts and parasites and with environmental conditions and landscape composition. Specific habitats often play an important role in parasite transmission (Lambin et al. 2010, Watts 2015). Landscape

composition affects population density and therefore interactions between parasites, primary hosts, intermediate hosts, and dead-end hosts (Park et al. 2013).

Moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) are examples of similar species sharing similar niches, with overlapping range along the southern boundaries of moose distribution in North America. Overlapping distributions of deer and moose are relatively recent in evolutionary terms, and there is growing evidence that niche differentiation has not yet evolved to the extent that moose populations can withstand interactions with sustained relatively high densities of deer (Lankester 2010). Since European settlement and range expansion by deer into moose range, there is a history of moose population declines in the presence of deer, and parasite transmission from deer to moose is believed to be a significant contributing factor in many instances (Whitlaw and Lankester 1994, Murray et al. 2006). However, the empirical evidence to support the implication that parasites transmitted from deer to moose cause moose population declines is lacking (Whitlaw and Lankester 1994, Lankester 2010, McGraw *chapter 1*).

Deer carry several parasites that cause morbidity and mortality in moose, which could lead to parasite-mediated competition through indirect interactions. Deer are the normal hosts of the giant liver fluke (*Fascioloides magna*) and meningeal worm (*Parelaphostrongylus tenuis*), both of which are believed to have contributed to historical and current declines of Minnesota moose populations (Murray et al. 2006, Wünschmann et al. 2015). In this paper we focus on the potential impacts of *P. tenuis* on moose because *P. tenuis* is implicated as a significant contributing factor in the current moose population decline in northeast Minnesota.

Moose becoming infected with *P. tenuis* is a critical step in a complex cycle of parasite-mediated competition between moose and deer. The probability of infection changes seasonally for moose and deer (Lankester and Peterson 1991), therefore there are biologically significant points of interaction that increase the risk of infection, specifically, regions where deer and gastropods co-occur, and where moose feed during snow-free seasons (Lankester and Peterson 1991). During winter, the probability of infection is zero for moose and deer because the gastropod intermediate hosts are unavailable under snow cover (Lankester and Peterson 1991). *P. tenuis* larvae are most prevalent on the landscape in early spring and summer after being deposited over winter in deer fecal pellets (Lankester and Anderson 1968). Gastropod intermediate hosts start to become infected in the spring after snow melt when they encounter *P. tenuis* larvae in deer fecal pellets and in the soil (Lankester and Anderson 1968). Larval development in gastropods into the infectious L3 stage takes between 30 to 60 days, depending on environmental conditions (Lankester and Anderson 1968). Therefore, prevalence on the landscape increases throughout summer and fall. If moose forage more often near the ground and in leaf litter in the fall and early winter they are more likely to consume gastropods, therefore it is likely that the probability of infection increases.

Where deer and moose are sympatric in the eastern United States and Canada, the landscape is dominated by boreal forests and northern hardwoods in the sub-boreal transition zones (Pastor and Mladenoff 1992). Moose and deer share similar dietary niches in the northern latitudes of deer range (Belovsky 1981, Rogers 1987), where browse is a significant proportion of deer diet in winter (45-91%) and during the summer (41-45%, Hewitt 2011). Moose diet largely consists of 25-30 species of woody plants in

any one location (Peek et al. 1976, Telfer 1978, Timmerman and McNicol 1988), and overlaps with deer diet. However, in management plans for moose (e.g., Minnesota Moose Research and Management Plan 2011), the potential shared food resources between deer and moose are often not addressed. In sympatric moose and deer range, habitat restoration for the benefit of moose often means the creation of young, regenerating forest patches with the intent of increasing forage for moose (Minnesota Moose Research and Management Plan 2011). Because of the significant woody browse component of northern deer population diets, these moose habitat restoration initiatives could result in increased co-occurrence of moose and deer, thus increasing the likelihood of indirect parasite-mediated competitive interactions in areas with shared forage resources.

Our objective was to evaluate the relative probability of co-occurrence between moose and deer at several time periods that could lead to parasite-mediated competition. Deer shed *P. tenuis* larvae year-round, but significantly more larvae are shed by deer during the winter (Lankester and Peterson 1996). Therefore, we estimated the relative probability of co-occurrence between active moose and deer during the spring, summer, and fall. We estimated the relative probability of co-occurrence between moose during non-snow seasons and deer in winter when they are shedding the most *P. tenuis* larvae. This research contributes to a growing body of literature regarding the likelihood of biologically meaningful interactions between moose and deer, as well as lends support to the theory that the moose-deer-*P. tenuis* system could be frequency dependent rather than density dependent and driven by shared resources that contribute to high contact rates between moose and deer.

Study Area

The study area (570-km^2) was located in northeastern Minnesota, USA (centered on latitude: 47° 37’ 30” N, longitude: 91° 24’ 57.6” W). The spatial extent of the study area was determined by the area of overlap between locations for global positioning system (GPS) collared moose and deer, obtained in a joint study of moose and deer resource selection (McGraw et al. *in prep*, Figure 4.1). The area of overlap between collared moose and deer was smaller than the overall study area for deer (McGraw, *Chapter 2*) and the overall study area for moose (McGraw, *Chapter 3*). The climate is continental with moderate to severe winters and warm summers. July is the warmest month when the mean daily high temperature is 26°C (National Oceanic and Atmospheric Administration [NOAA] 2015). The coldest month is January, when the mean minimum daily temperature is -10°C (NOAA 2015). Annual snowfall regularly reaches 180-cm and snow is present from December to April.

The region is transitional from northern hardwood forests to the south to boreal forests to the north (Pastor and Mladenoff 1992). The Superior National Forest, along with smaller parcels of state, county, and tribal holdings constitute >80% of property ownership. Upland forests are dominated by a mixture of paper birch (*Betula papyrifera*), aspen (*Populus tremuloides*), balsam fir (*Abies balsamea*), white pine (*Pinus strobus*), red pine (*P. resinosa*), and jack pine (*P. banksiana*). Lowlands are predominately black spruce (*Picea mariana*) and tamarack (*Larix laricina*) conifer swamps with some northern white cedar (*Thuja occidentalis*, Minnesota Ecological Classification System 2008).

Aerial moose population surveys are conducted annually during January. The largest population was in 2006 when there were an estimated 8,840 moose. Since 2006 the moose population has declined to an estimated 3,030 animals (DelGiudice 2018). A moose hunt was conducted annually until 2013 when the Minnesota Department of Natural Resources (MN DNR) suspended moose hunting indefinitely in response to the declining population. Tribes initially suspended their moose harvest but have since resumed harvesting about 30 moose per year.

Hunting is the greatest source of mortality for deer in the fall across much of Minnesota and fall hunting mortality is a component of the population model. Due to a recent DPA re-alignment and low deer harvest within the study area historically, deer densities are not calculated (D'Angelo and Giudice 2016) but pre-fawn densities are estimated to be fewer than 1 deer/km^2.

Methods

Geographic Position System (GPS) data

Moose (n = 30) were monitored for two years beginning in mid-January 2011 using GPS radio collars (Lotek Wireless, Inc., Newmarket, Ontario, Canada) programmed to record location data at 20-minute intervals and to record activity data on internal collar activity loggers at 5-minute intervals. We monitored deer (n = 53) in northeast Minnesota for two years beginning in January 2013 using GPS radio collars (GPS PLUS Vertex Survey Iridium, Vectronic Aerospace GmbH, Berlin, Germany) programmed to record location data at 2-hour intervals. Of the 53 deer monitored, 28 deer home ranges were entirely within the moose study area from 2011-2012 (Figure 4.1). The

deer with home ranges within the moose study area were used in analysis of co-occurrence with moose (McGraw *chapter 2* and *chapter 3*).

We retained 3D GPS locations and 2D GPS locations for moose and deer with dilution of precision values ≤ 5 (Lewis et al. 2007, Bjørneraas et al. 2010). A second check of GPS locations was done by calculating out and back movement rates using the middle location of three consecutive locations. If movement rate to and from the middle location exceeded the maximum running speed of moose (55-km/hour, "Minnesota Mammals – Moose" MN DNR) or if movement rates exceeded the maximum running speed of deer (45-km/hour, Hewitt 2011), the locations were removed for each (Street et al. 2015).

Defining seasons and periods of co-occurrence

We defined four seasons (winter, spring, summer, and fall) for moose using behavior patterns and climate conditions with biological relevance to moose (McGraw, *chapter 3*; Table 4.1). During each season, we also partitioned moose location data into active or inactive behaviors using activity logger data (McGraw, *chapter 3*) to address questions of co-occurrence between moose and deer that could lead to disease transmission (i.e. when moose were active and likely to be foraging). We defined two seasons (e.g., winter and summer) for deer using migration patterns (McGraw, *chapter 2*). We also combined seasonal locations of deer to analyze relative probability of use on an annual time scale because deer shed *P. tenuis* larvae throughout the year, and therefore there is a risk to moose becoming infected with *P. tenuis* when moose occur in an area during snow-free seasons where deer have occurred at any point in the year.

Habitat characteristics

We characterized land cover at a coarse spatial scale using land cover data from the National Land Cover Dataset (NLCD 2011; Homer et al. 2015, McGraw, *chapter 2 & chapter 3*). The NLCD has 16 land cover types. Woody wetlands, deciduous forest, mixed forest, coniferous forest, and shrub stands are the dominant land cover types and constituted 95% of the study area (Table 4.2). The remaining 11 land cover types were various types of human developments and other areas of little biological value to moose or deer, which when combined into the "other" land cover category summed to about 5% of the study area.

LiDAR data was used to provide measures of canopy height, canopy density, and understory density across coarse land cover classes (McGraw, *chapter 2 & chapter 3*). Canopy height was derived from the 75th percentile of point cloud heights. We used the 75th percentile rather than the highest points to reduce the potential influence of super-canopy white pines that occur in mixed forests and coniferous forests. Canopy cover was calculated as the proportion of non-ground returns above 3-m. An index of understory density was calculated by subtracting the proportion of non-ground returns above 1-m from the proportion of non-ground returns above 3-m.

Resource selection modeling for moose and deer

In chapters two and three we assembled a set of candidate Resource Selection Function (RSF) models for moose and deer, respectively, where land cover type was a categorical variable with woody wetlands used as the reference category, and canopy height, canopy cover, and understory density were continuous covariates (McGraw, *chapter 2 & chapter 3.*). RSF's were analyzed at the 3rd order of selection (Manly et al.

2002) where used points for each animal were represented by GPS locations within 95% kernel seasonal home ranges, and one random point per GPS location for each animal was generated within home ranges to represent available habitat components. We assessed goodness-of-fit of the top models (McGraw, *chapter 2 & chapter 3.*) using a 5-fold *k*-fold cross validation with Spearman's rank correlation (Boyce et al. 2002, Weins et al. 2008). Top models were the same for moose and deer in each season, with each model including land cover and each of the forest structural components (McGraw, *chapter 2 & chapter 3*). The resulting coefficient values from the best seasonal RSF models for moose (McGraw *chapter 2*) and deer (McGraw *chapter 3*) were used to estimate co-occurrence.

Relative probabilities of co-occurrence between moose and deer

We estimated the relative probability of co-occurrence between moose and deer following Courbin et al. (2009), to understand the potential for biologically significant overlap in resource use that could lead to resource competition or parasite-mediated competition. For resource competition, we focused on winter and summer for both species. The important time periods for potential parasite-mediated competition between moose and deer include when moose were active in snow-free seasons, and where deer occurred annually. Deer shed more *P. tenuis* larvae in winter, and so another calculation of co-occurrence was made where deer occurred in winter versus where moose occurred and were active in snow-free seasons (Table 4.3).

The relative probability of co-occurrence between moose and deer was estimated using final RSF's from the set of annual, winter, and summer models for deer (McGraw *chapter 3*), and the set of all moose seasonal models and seasonal active moose models

(McGraw *chapter 2*). From the RSF models obtained for deer in chapter 2 and for moose in chapter 3, we created a set of predictive maps of relative probability of occurrence (i.e. RSF values) for each species within the overlapping region of the study areas (Figure 4.1), using the equation:

$$(1)\ w(x) = \exp\left(\beta_{1ij}x_{1ij} + \cdots + \beta_{nij}x_{nij} + \gamma_{0\mathrm{j}}\right)$$

where $w(x)$ is the relative probability of occurrence, B_i are the log odds coefficient values, x_{1ij} are the coefficients, and $\gamma_{0\mathrm{j}}$ is the random intercept for individual animals. Each set of predicted RSF values *w(x)* was scaled between 0 and 1 (Courbin et al. 2009) for both species:

$$(2)\ \widehat{w} = \left(\frac{w(x) - w_{min}}{w_{max} - w_{min}}\right)$$

where *w(x)* was the relative probability of use by either moose or deer for each 30 x 30-m pixel within the study area. The smallest RSF value in a pixel for each species, respectively, was w_{min} and the largest RSF value was w_{max}. The scaled deer and moose RSF values of each 30 x 30-m pixel in the study area were multiplied to estimate the relative probability of co-occurrence (Courbin et al. 2009):

$$(3)\ \widehat{w}_{co} = \widehat{w}_{moose} \times \widehat{w}_{deer}$$

where $\widehat{w}_{moose}$ is the relative probability of occurrence of moose, $\widehat{w}_{deer}$ is the relative probability of occurrence of deer, and $\widehat{w}_{co}$ is the relative probability of co-occurrence. Co-occurrence estimates were also scaled between zero and one (Courbin et al. 2009).

To examine the ecological factors that contribute to high relative probability of co-occurrence of moose and deer in the study area we classified each pixel into terciles

based on $\widehat{w}_{co}$. We further calculated the proportion of each land cover type in each of those terciles and across the entire study area, and the values of the forest structural metrics were summarized to contrast the habitat attributes in areas with the highest probability of co-occurrence (the upper tercile) with the areas with the lowest probability of co-occurrence (the lower tercile).

Results

Relative probability of co-occurrence between moose and deer in summer

The highest relative probability of deer and moose co-occurring in summer was in deciduous forests, mixed forests, and shrub stands (Figure 4.2, Figure 4.3). During the summer, moose and deer were least likely to co-occur in conifer forests, woody wetlands, and the 'other' land cover type category. Deciduous forests, mixed forests, and shrub stands composed 91% of the total area of highest relative probability of co-occurrence in summer, compared to 28% across the entire study area (Table 4.4).

During the summer, distributions of LiDAR variables overlapped between tercile areas of highest and lowest probability of co-occurrence (Figure 4.3). For each of these variables, the distribution across the area of co-occurrence overlapped, and the range was similar. For example, mean canopy height was 4.0-m (range: 1.0-26.0-m) and 4.3-m (range: 1.0-27.0-m) for areas with the highest probability of co-occurrence and areas with the lowest probability of co-occurrence, respectively. The proportion of canopy cover per pixel was 44% (range: 0-92%) and 49% (range: 0-94%) in the areas of highest and lowest relative probability of co-occurrence, respectively. Finally, the proportion of understory density per pixel was 11% (range: 0-62%) and 14% (range: 0-100%) for areas with the highest and lowest relative probability of co-occurrence, respectively.

Relative probability of co-occurrence between moose and deer in winter

In winter, the relative probability of co-occurrence of moose and deer was also highest in deciduous forest, mixed forest, and shrub stands (Figure 4.3). Moose and deer had the lowest relative probability of co-occurrence in coniferous forests, woody wetlands, and the 'other' land cover type. Deciduous forest, mixed forest, and shrub stands comprised 85% of the area with the highest relative probability of occurrence, but only 28% of the entire study area (Table 4.5).

During the winter, distributions of LiDAR variables overlapped in range between tercile areas of highest and lowest probability of co-occurrence. For example, mean canopy heights were 7.0-m (range: 1.0-20.0-m) in areas with the highest relative probability of co-occurrence while canopy heights in areas with the lowest probability of co-occurrence were 12.1-m (range: 1.0-28.0-m, Figure 4.3). In the areas of highest relative probability of co-occurrence canopy cover was 60% (range: 0-94%) while in areas of lowest relative probability of co-occurrence average canopy cover was 40% (range: 0-81%, Figure 4.3). Understory density in areas of the highest relative probability of co-occurrence was 15% (range: 0-100%) while understory density areas with the lowest relative probability of co-occurrence was 8% (range: 0-36%).

Spring, summer, and fall habitat selection by active moose versus annual habitat selection by deer: Relative probability of co-occurrence

The areas of highest relative probability of co-occurrence appeared to be similar between deer at an annual scale and moose during spring, summer, and fall in terms of cover type selection. The areas of the highest relative probability of co-occurrence were deciduous forests and mixed forests in spring, summer, and fall (Figure 4.4, Figure 4.5).

During the summer and fall, the areas with the highest relative probability of co-occurrence also included shrub stands (Figure 4.4, Figure 4.7). The lowest relative probability of co-occurrence was in woody wetlands during all snow-free seasons and conifer forests during the spring and fall.

During the spring, deciduous forests and mixed forests accounted for 79% of the area with the highest relative probability of co-occurrence while accounting for just 22% of the entire study area (Table 4.5). Deciduous forests, mixed forests, and shrub stands accounted for 68 - 93% of the area with the highest relative probability of co-occurrence and 24 - 26% of the study area during the summer and fall (Table 4.5).

While the range of LiDAR variables overlapped between tercile areas of highest and lowest probability of co-occurrence, there appeared to be differences in the average values of LiDAR variables between tercile areas. For example, during the spring, the areas of highest relative probability of co-occurrence had average canopy heights of 9.0-m (range: 1.0-26.0-m), 44% canopy cover (range: 0-83%), and 14% understory density (range: 0-100%). In contrast, areas with the lowest relative probability of co-occurrence (Figure 4.5) had average canopy heights of 11.0-m (range: 1.0-28.0-m), average canopy cover of 60% (range: 3-94%), and average understory density of 8% (range: 1-34%). In the summer the areas with the highest relative probability of co-occurrence had average canopy heights of 9.0-m (range: 1.0-27.0-m), 40% canopy cover (range: 0-69%), and 11% understory density (range: 0-63%), while areas with the lowest relative probability of co-occurrence (Figure 4.5) had average canopy heights of 8.0-m (range: 1.0-26.0-m), average canopy cover of 49% (range: 0-94%), and average understory density of 14% (range: 0-100%). The areas of highest relative probability of co-occurrence in the fall had

average canopy heights of 7.0-m (1.0-27.0-m), 35% canopy cover (range: 0-81%), and 12% understory density (12%, range: 0-63%) while areas of lowest relative probability of co-occurrence (Figure 4.5) had average canopy heights of 11.0-m (range: 3.0-27.0-m), average canopy density of 68% (range: 38-94%), and average understory density of 11% (range: 0-53%).

Snow-free season habitat selection by active moose versus winter habitat selection by deer: Relative probability of co-occurrence

During a period of potential overlap in habitat use between deer in winter and moose in the spring, the areas with the highest relative probability of co-occurrence were deciduous forests and mixed forests (Figure 4.6, Figure 4.7). Areas with the lowest probability of co-occurrence in the spring were woody wetlands, conifer forests, and shrub stands (Figure 4.7). The areas of highest relative probability of co-occurrence during winter for deer and summer for active moose also were deciduous forests and mixed forests, but included shrub stands, which was different from areas occupied by moose in the spring (Figure 4.7). The areas of lowest relative probability of co-occurrence were woody wetlands, conifer forests, and the 'other' land cover type during the summer. Patterns of relative probability of co-occurrence appeared to be most different in the fall when areas of highest probability of co-occurrence included only woody wetland and shrub stands (Figure 4.7). The areas with the lowest probability of co-occurrence for deer in the winter and moose in the fall were conifer forests.

During the spring, deciduous forests and mixed forests account for 55% of the area with the highest relative probability of co-occurrence and 21% of the entire study area (Table 4.6). Deciduous forests, mixed forests, and shrub stands accounted for 94%

of the area with the highest relative probability of co-occurrence in the summer and 24% of the study area (Table 4.6). In the fall, shrub stands and woody wetlands constituted 74% of the area with the highest probability of co-occurrence and 22% of the study area (Table 4.6).

Discussion

Mutual selection and mutual avoidance of resource units seem to be the driving forces behind biologically significant interactions between moose and deer. Our study demonstrates that coarse land cover components and fine-scale forest structural components of the habitat influenced the occurrence of moose and deer in such a way that co-occurrence was predominately in areas that were most likely to supply food and was not in areas that were most likely to provide thermal cover. Co-occurrence in areas that supply forage could be contributing to parasite-mediated competition. We found that deer and moose also showed similar patterns of resource avoidance in some seasons, specifically avoidance of conifer, the 'other' cover type, and woody wetlands. Mutual avoidance of resources by deer and moose might also be contributing to higher effective densities of moose and deer in some of the landscape, which would contribute to increased opportunity for parasite-mediated competition.

Similarities in habitat selection between moose and deer: direct co-occurrence

Similarities in habitat selection at coarse and fine scales by moose and deer may result in co-occurrence at foraging sites throughout the year in northeast Minnesota. In each season, similarities in selection resulted in the highest probability of co-occurrence in habitats most likely to serve as foraging habitat. Moose show strong preference for

deciduous and mixed deciduous stands where food is abundant (Dussault et al. 2005). Additionally, shrub stands in northeast Minnesota are deciduous, and can contain species frequently browsed by moose and deer, including red osier dogwood (*Cornus sericea*), hazelnut (*Corylus americana*), and young, regenerating aspen, birch, and cherries (*Prunus virginiana* and *P. pensylvanica*, Crawford 1982, Rogers 1987, Ward 2015). In deciduous and mixed forest stands, less dense canopies as a result of timber harvest and naturally formed canopy gaps allow for light penetration into the sub canopy and shrub layers, and thus increased productivity of those layers (Lieffers et al. 1998), which would lead to increased forage availability.

It does not appear that resource partitioning to reduce competitive interactions occurred during the summer when deer and active moose selected deciduous forests (McGraw *chapter 2* and *chapter 3*). A moose's day is partitioned into bouts of foraging and resting and ruminating, with <5% of their daily time budget allocated to other behaviors (Risenhoover 1986, Cederlund 1989, Van Ballenberghe and Miquelle 1990). Therefore, when moose select deciduous stands during periods of activity during the summer, it is presumably because they are foraging in those stands (McGraw *chapter 3*).

During the winter moose avoided taller canopies and canopy cover when active and inactive (McGraw *chapter 3*), while deer either selected or used them in proportion to availability. Deer in northern latitudes seek thermal cover and relief from deep snow, which is offered by denser canopies that interrupt snow-fall and provide cover from wind (Tierson et al. 1985, Van Deelen et al. 1998). In northern latitudes where moose and deer range overlap, winter temperatures regularly exceed those associated with causing thermal stress in moose (Renecker and Hudson 1986, McCann et al. 2013), and moose

will avoid canopy cover (Schwab and Pitt 1991) to gain thermal relief through radiant heat loss (McCann et al. 2016).

Similarities in habitat selection between moose and deer: potential for parasite-mediated competition

Shared food resources often result in sustained contact between host species in host-parasite systems (Watts 2015, Hartemink et al. 2014, Becker and Hall 2014), which appears consistent with the moose-deer-*P. tenuis* system. Unlike deer, moose are more strictly browsers, with a vertical feeding range typically defined between 0.5 - 2.8-m, regardless of season. However, in the spring moose occasionally forage on or near the ground on ephemeral herbaceous plants (Shipley 2010, Renecker and Hudson 1986, Timmerman and McNicol 1988), which could increase their risk of ingesting gastropods.

While deer feeding low to the ground is mentioned often in the literature as the most probable location of acquiring infected gastropods (Lankester and Peterson 1991, Peterson et al. 1996), the same suggestion is not explicitly made for moose. Moose forage predominantly in the understory shrub layer during summer when browse is abundant. A shift to foraging more closely to the ground on leaf litter during fall by moose has been documented once (Renecker and Hudson 1986). It is possible moose feed more often in the litter layer in the fall, but if so, that behavior has been underreported. If it is the case that moose spend a significant amount of time foraging in the litter layer in the fall, then the route and timing of infection would mirror that of deer (Peterson et al. 1996).

Conclusions

Relative probability of co-occurrence between moose and deer was highest in areas that were likely providing forage, regardless of interaction type. There was little evidence of resource partitioning between moose and deer that would lessen interactions around food resources except potentially in the fall when moose avoided forested cover types relative to woody wetlands (McGraw *chapter 3*) while deer selected them (McGraw *chapter 2*).

Areas with the highest relative probability of deer occurrence were in habitats shared by moose and more likely to provide food than shelter (McGraw *chapter 2* and *chapter 3*). Pre-fawn deer densities within the study area were estimated to be between 1-2 deer/km^2 (D'Angelo and Giudice 2016). But, if deer are most likely to occur on just 30% of the landscape, then the effective deer density in our study area might be closer to 6 deer/km^2. While this estimate is not precise, we use it to make the point that relating populations to habitats using resource selection functions (Boyce and McDonald 1999) should be an avenue of future research in regions where moose and deer overlap to estimate effective deer and moose densities where co-occurrence is most likely.

Habitat restoration initiatives for the benefit of moose will also have benefits for deer and management efforts to encourage resource partitioning are likely not possible in regions where deer and moose diets are closely aligned. There is a belief that large cut-over areas are a benefit to moose because they provide abundant deciduous shrubs that are a main food source for moose (Crête 1989), and that deer, being an edge species (Williamson and Hirth 1985) are reluctant to use large clear-cuts. However, the food benefit of cut-over areas is restricted to 15-40 years following the disturbance

(Franzmann and Schwartz 1985), and moose densities in large cut-over areas are generally low (Girard and Joyal 1984, Courtois et al. 2002). By comparison, deer will forage throughout smaller-sized clear-cuts (Williamson and Hirth 1985). Because moose and deer will both utilize clear-cuts, we recommend that future research into the potential for habitat partitioning between moose and deer invest in producing remotely sensed datasets that include forest patch sizes, stand ages, and type of disturbance to better understand whether certain types of forest disturbances are preferred or avoided by moose or deer.

Table 4.1. Season dates by year used in the analysis of deer and moose relative probability of co-occurrence. Seasons were identified by climate patterns and biological relevance to moose, which resulted in slight differences in dates between year, but allowed us to pool locations across years, by season. Deer data was pooled across the entire year to estimate resource selection functions at the annual scale but was also truncated to include only February - May for analysis of resource selection to estimate deer occurrence at the time of year when deer shed the most P. tenuis larvae.

Species	Season	Start Date	End Date
Deer	Annual	01/01/2014	12/31/2014
		01/01/2015	10/15/2015*
	Winter	01/01/2014	4/28/2014
		12/04/2014	4/19/2015
	Summer	04/29/2014	12/3/2014
		4/18/2015	10/15/2015*
Moose	Winter	01/25/2011	4/23/2011
		11/26/2011	3/16/2012
	Spring	04/24/2011	05/15/2011
		03/17/2012	05/15/2011
	Summer	06/07/2011	09/05/2011
		06/07/2012	09/04/2012
	Fall	09/06/2011	11/25/2011
		09/15/2012	11/23/2012

*Ended because of the number of collar failures and lack of sample size

Table 4.2. Covariates used to develop resource selection function (RSF) models for moose in northeast Minnesota at multiple scales of selection (McGraw *chapter 2 & chapter 3*).

Predictor Variable	Proportion Available	Description
Land Cover		
Woody Wetlands	0.38	>20% of vegetation cover is either forest or shrub and soil is periodically covered in water or saturated
Deciduous Forest	0.06	>20% total vegetation cover and >75% of trees shed foliage simultaneously because of seasonal change
Coniferous Forest	0.24	>20% total vegetation cover and >75% of tree species maintain leaves all year so that the canopy always maintains green foliage
Mixed Forest	0.17	>20% total vegetation cover and neither deciduous or conifer are >75% of canopy cover
Shrub	0.10	>20% total vegetation cover and includes true shrubs and young trees
Other	0.05	Remaining cover types that, individually, comprise 5% of the landscape; includes developed cover types, agriculture, and emergent wetlands
Canopy height	--	Height 75^{th} percentile
Canopy density	--	Percent of vegetation returns > 3 m
Understory	--	Percent of vegetation returns 1 - 3 m

Table 4.3. The combinations of calculations of relative probability of co-occurrence between moose and deer that could lead to resource competition, and calculations of the relative probability of co-occurrence between moose and deer that could lead to parasite-mediated competition through disease transmission from deer to moose. Relative probability of co-occurrence for the combinations of seasons for moose and deer were calculated using $\widehat{w}_{co} = \widehat{w}_{moose} \times \widehat{w}_{deer}$, where $\widehat{w}_{moose}$ is the relative probability of occurrence of moose and $\widehat{w}_{deer}$ is the relative probability of occurrence of deer. Probabilities of occurrence were derived using RSF models (McGraw, *chapter 2 & 3*).

Comparisons of co-occurrence	
Moose	Deer
Winter	Winter
Summer	Summer
Spring, Active	Annual
Summer, Active	Annual
Fall, Active	Annual
Spring, Active	Winter
Summer, Active	Winter
Fall, Active	Winter

Table 4.4. Area (km^2) of each land cover type in the entire study area, and in areas within the study site that have the higher relative probability of co-occurrence between moose and deer in summer and winter (Upper columns). The columns labeled "Lower" contain land cover areas with the lowest relative probability of co-occurrence. Upper and lower refer to upper and lower terciles of relative probability of co-occurrence. There are no estimates of variance because these are total areas of land cover types within the study area and within upper and lower terciles.

NLCD	Study Site	Summer, Upper	Summer, Lower	Winter, Upper	Winter, Lower
Woody Wetlands	0.38	0.00	0.92	0.10	0.52
Deciduous	0.06	0.20	0.00	0.12	0.00
Conifer	0.24	0.05	0.05	0.05	0.39
Mixed Forest	0.17	0.52	0.00	0.41	0.00
Shrub	0.10	0.19	0.00	0.32	0.00
Other	0.05	0.05	0.03	0.00	0.09
Proportion study site		0.31	0.35	0.29	0.34
Area (km^2) of study site	345	106	119	99	119

Table 4.5. Proportion of each land cover type in the study area, and in areas within the study site that have the highest relative probability of co-occurrence between moose and deer for moose in spring, summer, and fall, versus where deer were annually (Upper tercile columns). The columns labeled "Lower" contain land cover areas with the lowest relative probability of co-occurrence (lower tercile). Upper and lower refer to upper and lower terciles of relative probability of co-occurrence. There are no estimates of variance because these are total areas of land cover types within the study area and within upper and lower terciles.

NLCD	Study Site	Spring Upper	Spring Lower	Summer Upper	Summer Lower	Fall Upper	Fall Lower
Woody Wetlands	0.38	0.05	0.55	0.00	0.88	0.21	0.73
Deciduous	0.06	0.22	0.00	0.21	0.00	0.09	0.00
Conifer	0.24	0.03	0.39	0.03	0.08	0.05	0.27
Mixed Forest	0.17	0.57	0.00	0.46	0.00	0.33	0.00
Shrub	0.10	0.05	0.05	0.26	0.00	0.26	0.00
Other	0.05	0.08	0.00	0.04	0.04	0.06	0.00
Proportion of study site		0.28	0.39	0.26	0.38	0.38	0.11
Area (km^2)	345	97	134	89	133	132	37

Table 4.6. Proportion of each land cover type in the study area, and in areas within the study site that have the highest relative probability of co-occurrence between moose and deer for moose in spring, summer, and fall, versus where deer were in the winter (Upper tercile columns). The columns labeled "Lower" contain land cover areas with the lowest relative probability of co-occurrence (lower tercile). Upper and lower refer to upper and lower terciles of relative probability of co-occurrence. There are no estimates of variance because these are total areas of land cover types within the study area and within upper and lower terciles.

NLCD	Study Site	Spring Upper	Spring Lower	Summer Upper	Summer Lower	Fall Upper	Fall Lower
Woody Wetlands	0.38	0.34	0.13	0.00	0.78	0.40	0.32
Deciduous	0.06	0.16	0.00	0.20	0.00	0.05	0.05
Conifer	0.24	0.06	0.60	0.06	0.14	0.03	0.48
Mixed Forest	0.17	0.39	0.00	0.47	0.00	0.14	0.09
Shrub	0.10	0.03	0.19	0.27	0.00	0.33	0.01
Other	0.05	0.02	0.08	0.00	0.08	0.04	0.05
Proportion study site		0.37	0.15	0.25	0.42	0.29	0.45
Total km^2 of study site	345	128	52	88	144	99	156

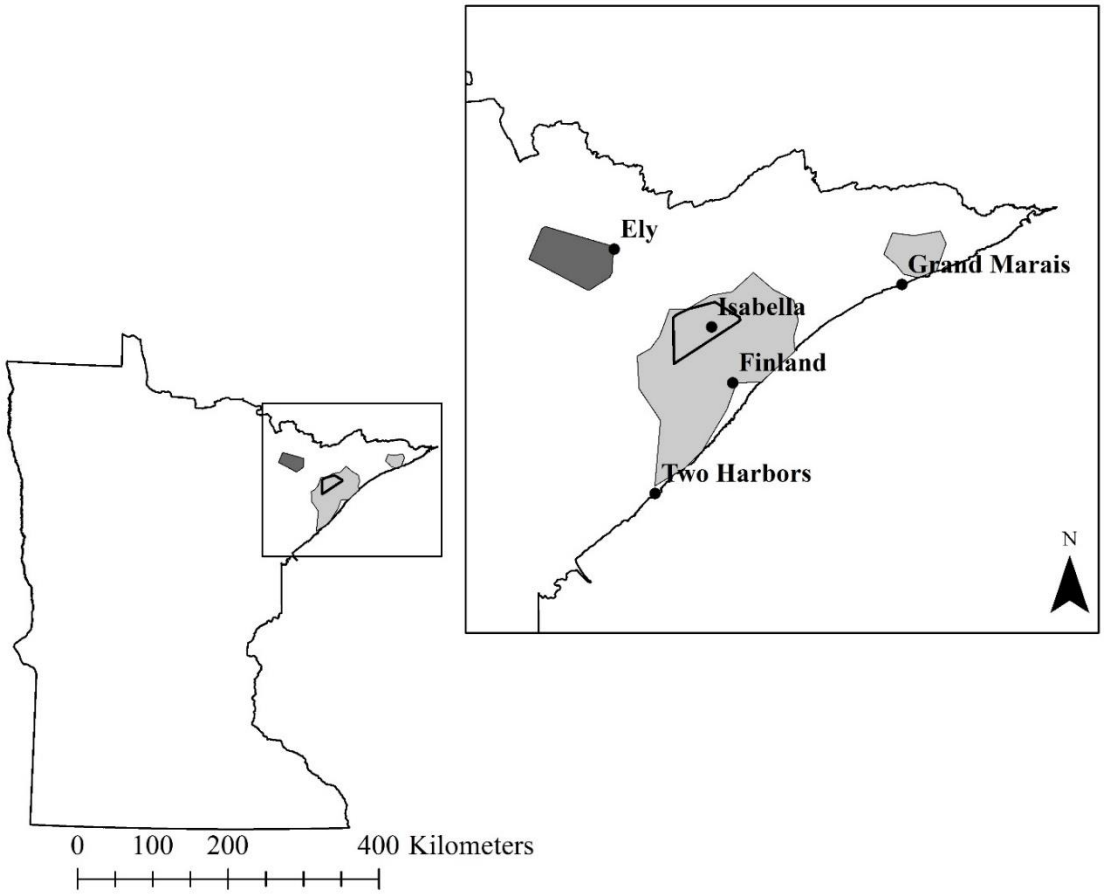


Figure 4.1. Study site where moose and deer study areas overlapped in northeast Minnesota. Light gray polygons are the moose study area from the 2011-2012 GPS collar study. The dark gray area and black outlined polygon within the moose study area in Isabella are the deer study sites from the 2014-2015 deer GPS collar study. The black outlined polygon within the moose study site at Isabella, MN is the area of overlap between the GPS locations of moose and deer from the joint studies that we restricted our analysis of co-occurrence to.

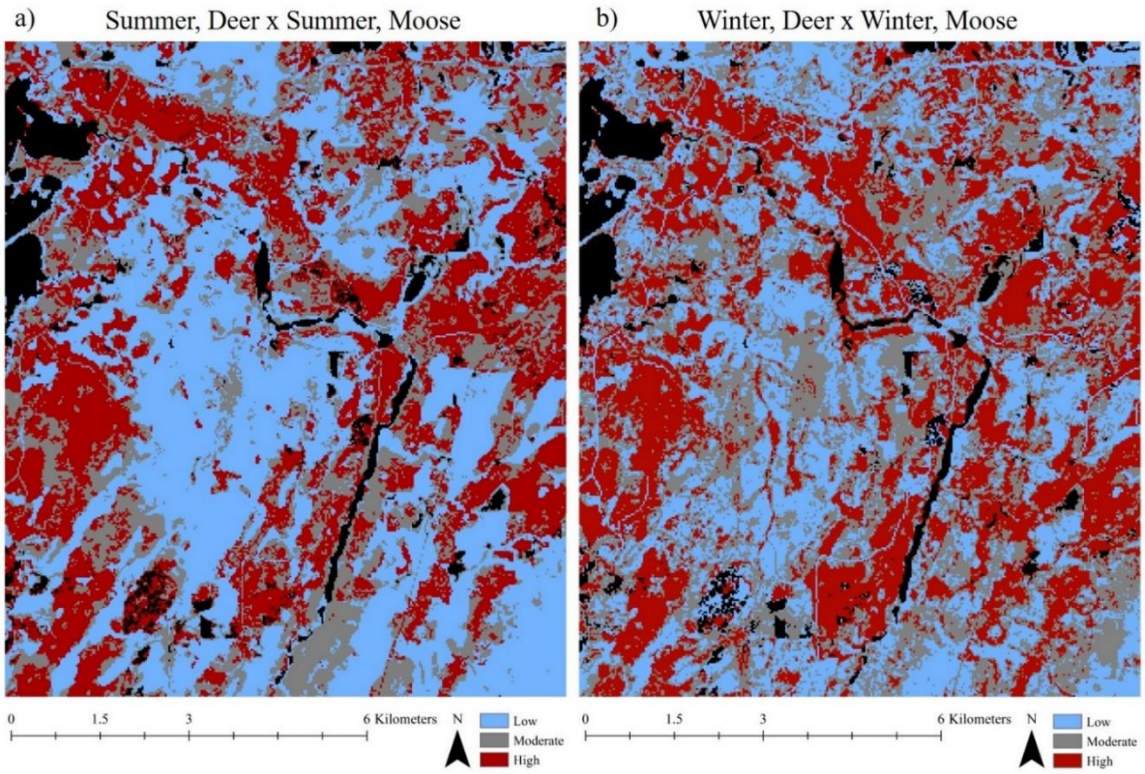
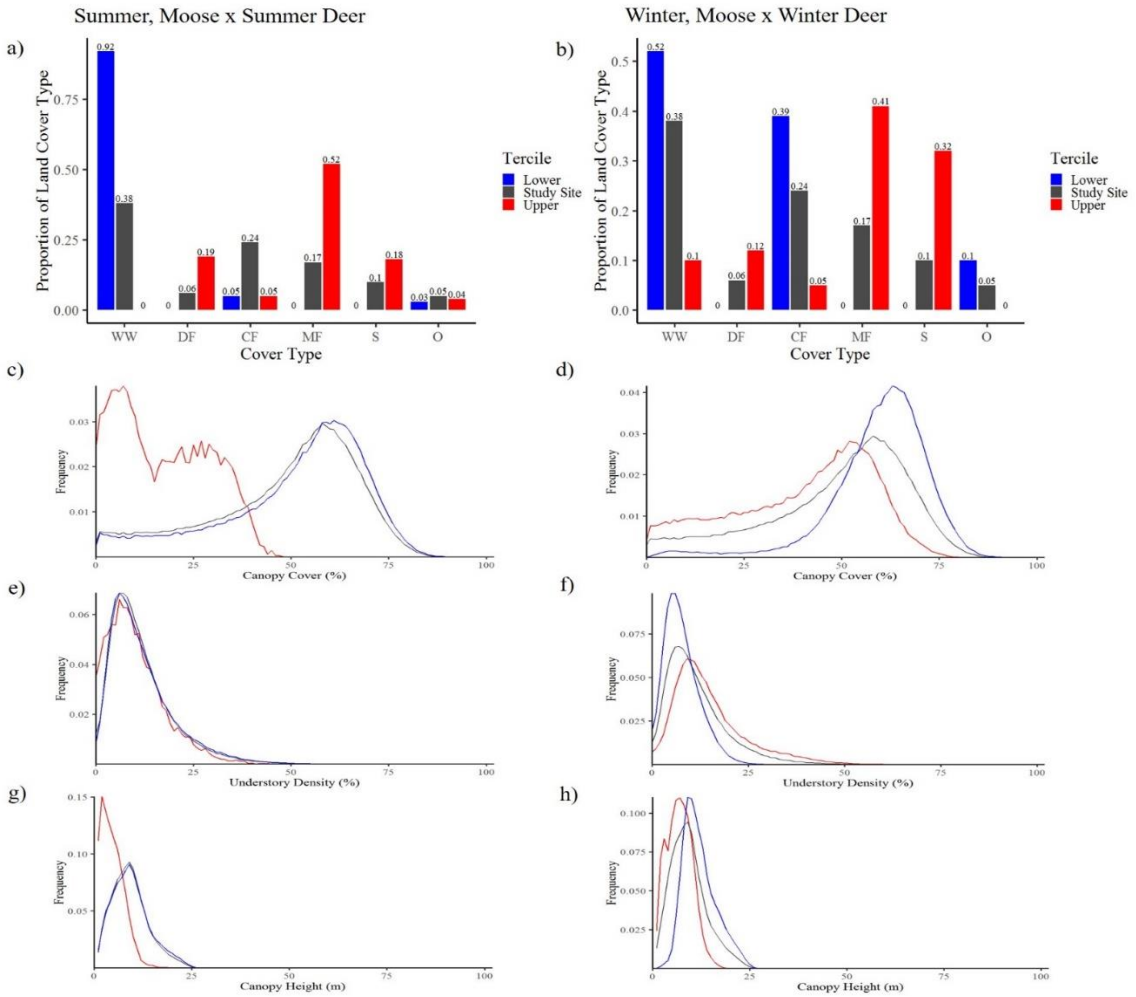


Figure 4.2. Relative probability of co-occurrence of moose and deer in summer (a) and winter (b). Relative probability of co-occurrence was assigned to tercile groups, with the upper tercile representing the areas with highest relative probability of co-occurrence and the lower tercile representing the areas lowest relative probability of co-occurrence. Red colors on the study area images represent the highest relative probability of co-occurrence between moose and deer. Blue colors on the study area image represent the lowest relative probability of co-occurrence between moose and deer. Black areas are open water. Moose and deer were most likely to co-occur in deciduous forests, mixed forests, and shrub stands in both winter and summer. In the summer moose and deer were least likely to co-occur in woody wetlands due to avoidance by deer. In winter, moose and deer were slightly more likely to co-occur in woody wetlands, which likely functioned as thermal cover for both species.



**WW = woody wetlands, DF = Deciduous Forest, CF = Conifer Forest, MF = Mixed Forest, S = Shrub, O = Other*

Figure 4.3. Relative probability of co-occurrence for moose and deer during summer and winter. Relative probability of co-occurrence was assigned to tercile groups, with the upper tercile representing the areas with highest relative probability of co-occurrence and the lower tercile representing the areas lowest relative probability of co-occurrence. Proportions of each land cover type in the upper tercile group (red bars) and lower tercile group (blue bars) of relative probability of co-occurrence between moose and deer in summer and winter are show relative to cover type availability within the study area (dark gray bars). Canopy cover, understory density and canopy height value frequencies are shown for each season. The red lines represent the frequency of forest structural components in the upper tercile where moose and deer were most likely to co-occur. The blue lines represent the frequency of forest structural component values in the lower tercile where moose and deer were least likely to co-occur. The gray lines represent the frequency of forest structural component values in the study site.

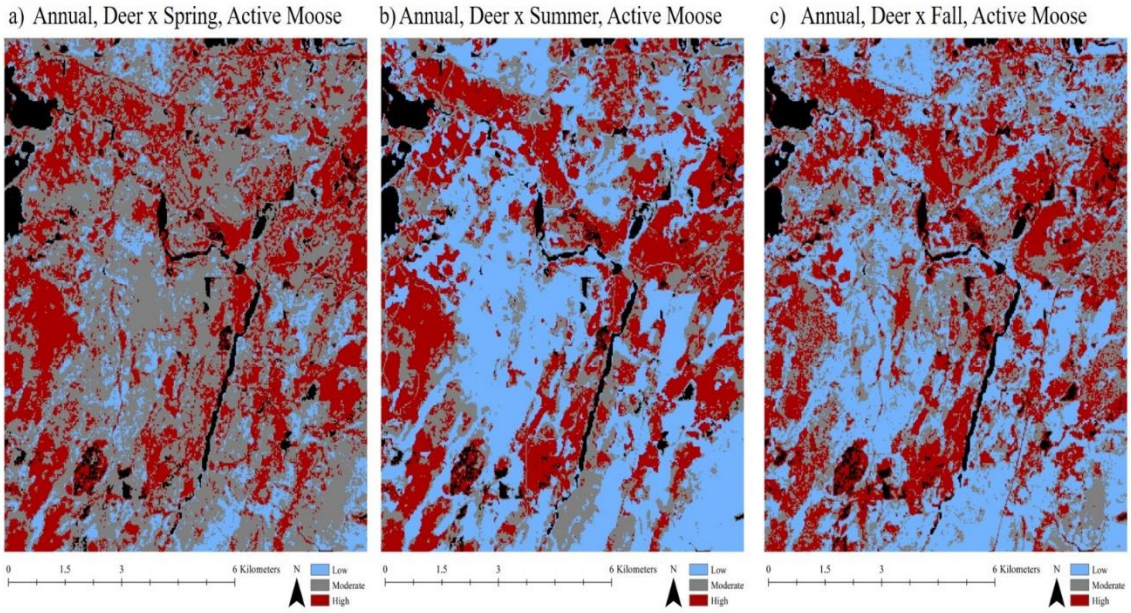
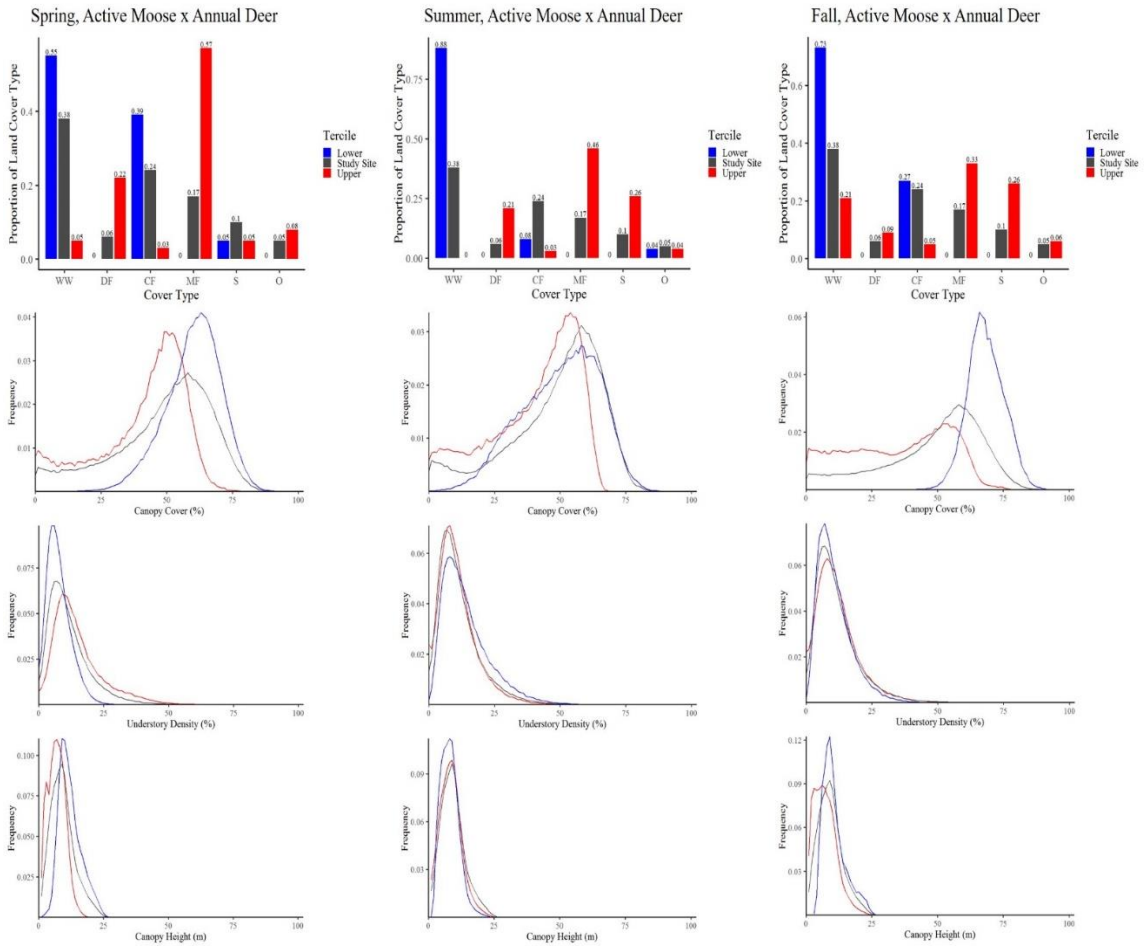


Figure 4.4. Relative probability of co-occurrence between deer at an annual scale and active moose during spring (a) summer (b), and fall (c), which represents areas that could lead to risk of disease transmission from deer to moose. Relative probability of co-occurrence was assigned to tercile groups, with the upper tercile representing the areas with highest relative probability of co-occurrence and the lower tercile representing the areas lowest relative probability of co-occurrence. Red colors on the study area images represent the highest relative probability of co-occurrence between moose and deer. Blue colors on the study area image represent the lowest relative probability of co-occurrence between moose and deer. Black areas are open water.



**WW = woody wetlands, DF = Deciduous Forest, CF = Conifer Forest, MF = Mixed Forest, S = Shrub, O = Other*

Figure 4.5. Relative probability of co-occurrence for active moose during spring, summer, and fall and for deer annual occurrence. Relative probability of co-occurrence was assigned to tercile groups, with the upper tercile representing the areas with highest relative probability of co-occurrence and the lower tercile representing the areas lowest relative probability of co-occurrence. Proportions of each land cover type in the upper tercile group (red bars) and lower tercile group (blue bars) of relative probability of co-occurrence between moose and deer in summer and winter are show relative to cover type availability within the study area (dark gray bars). Canopy cover, understory density and canopy height value frequencies are shown for each season. The red lines represent the frequency of forest structural components in the upper tercile where moose and deer were most likely to co-occur. The blue lines represent the frequency of forest structural component values in the lower tercile where moose and deer were least likely to co-occur. The gray lines represent the frequency of forest structural component values in the study site.

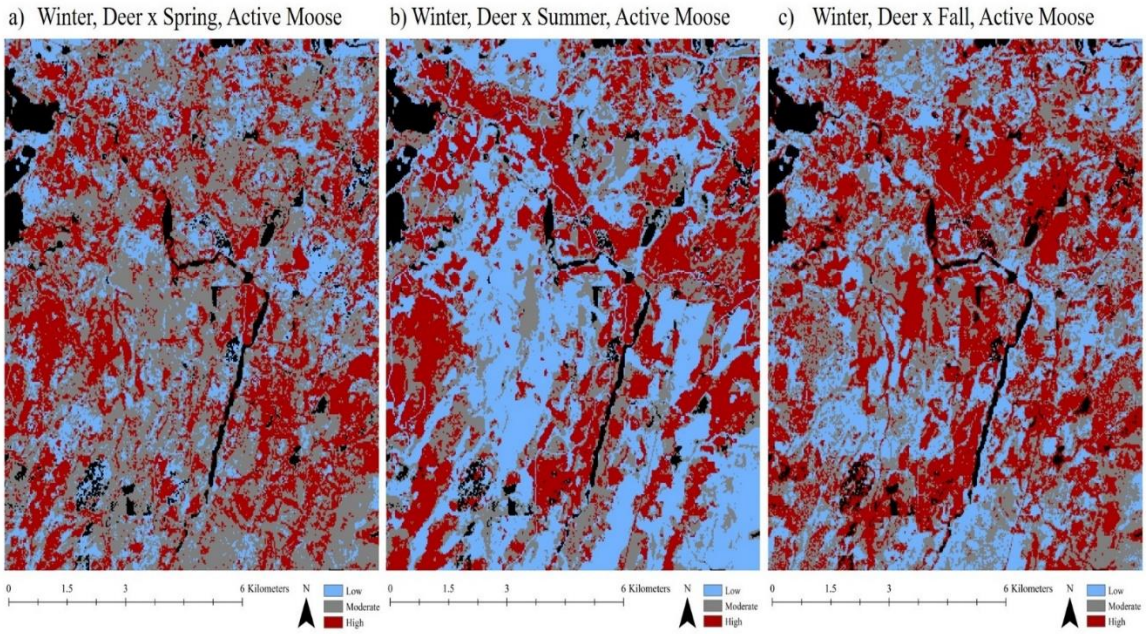
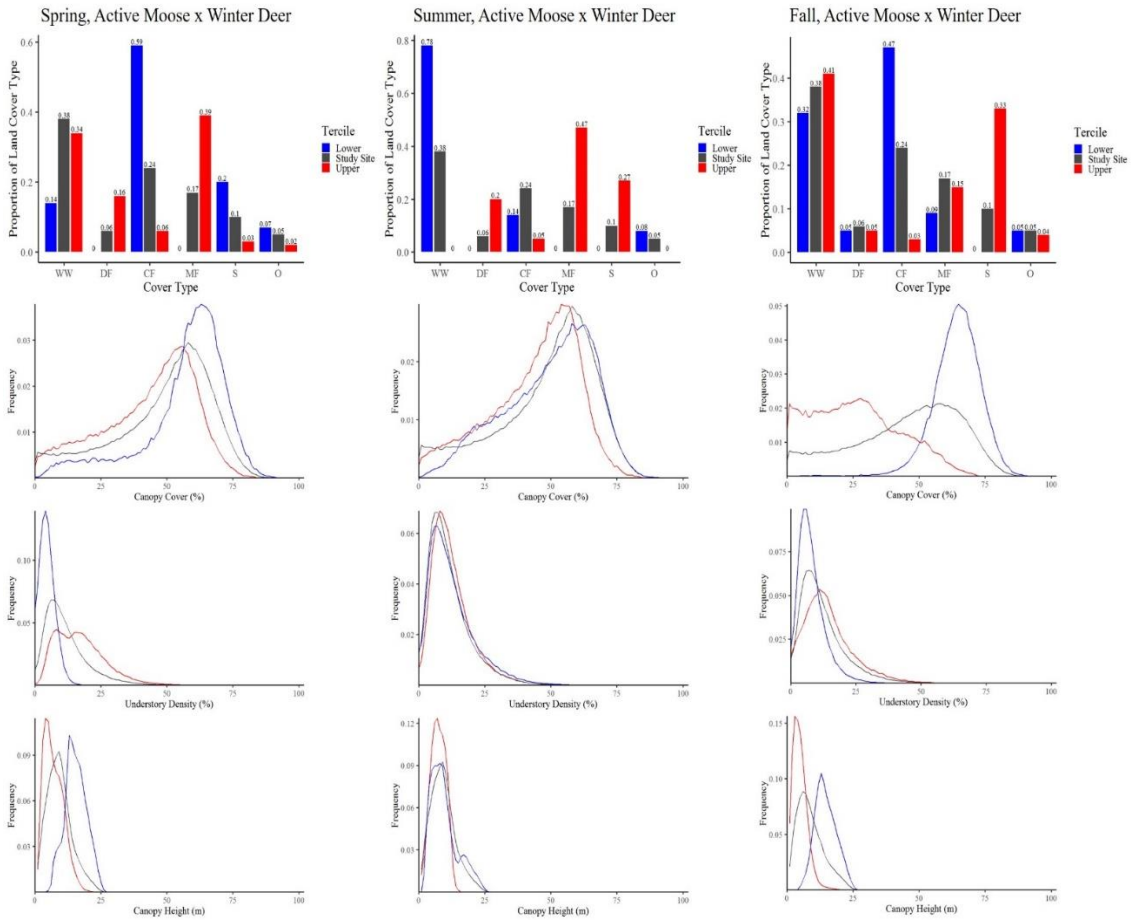


Figure 4.6. Relative probability of co-occurrence between deer during winter and active moose during spring (a) summer (b), and fall (c), which represents areas that could lead to the highest risk of disease transmission from deer to moose. Relative probability of co-occurrence was assigned to tercile groups, with the upper tercile representing the areas with highest relative probability of co-occurrence and the lower tercile representing the areas lowest relative probability of co-occurrence. Red colors on the study area images represent the highest relative probability of co-occurrence between moose and deer. Blue colors on the study area image represent the lowest relative probability of co-occurrence between moose and deer. Black areas are open water.



**WW = woody wetlands, DF = Deciduous Forest, CF = Conifer Forest, MF = Mixed Forest, S = Shrub, O = Other*

Figure 4.7. Relative probability of co-occurrence for active moose during spring, summer, and fall and for deer during winter. Relative probability of co-occurrence was assigned to tercile groups, with the upper tercile representing the areas with highest relative probability of co-occurrence and the lower tercile representing the areas lowest relative probability of co-occurrence. Proportions of each land cover type in the upper tercile group (red bars) and lower tercile group (blue bars) of relative probability of co-occurrence between moose and deer in summer and winter are show relative to cover type availability within the study area (dark gray bars). Canopy cover, understory density and canopy height value frequencies are shown for each season. The red lines represent the frequency of forest structural components in the upper tercile where moose and deer were most likely to co-occur. The blue lines represent the frequency of forest structural component values in the lower tercile where moose and deer were least likely to co-occur. The gray lines represent the frequency of forest structural component values in the study site.

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